WATSONIA

Journal and Proceedings of the Botanical
Society of the British Isles

Volume 15 Part 3 February 1985
Editors: J. R. Akeroyd, S. M. Eden,
R. J. Gornall, N. K. B. Robson

ISSN: 0043-1532

Botanical Society of the British Isles

Patron: Her Majesty Queen Elizabeth the Queen Mother

Applications for membership should be addressed to the Hon. General Secretary, c/o Department of Botany, British Museum (Natural History), Cromwell Road, London, SW7 5BD, from whom copies of the Society's Prospectus may be obtained.

Officers for 1984-85

Elected at the Annual General Meeting, 19th May 1984

President, Mr J. F. M. Cannon

Vice-Presidents, Mr R. W. David, Mr E. C. Wallace, Dr S. M. Walters, Professor D. A. Webb

Honorary General Secretary, Mrs M. Briggs

Honorary Treasurer, Mr M. Walpole

Honorary Editors, Dr J. R. Akeroyd, Dr S. M. Eden, Dr R. J. Gornall, Dr N. K. B. Robson, Dr B. S. Rushton (*Watsonia*); Mr D. H. Kent (*B.S.B.I. Abstracts*); Mr E. D. Wiggins (*B.S.B.I. News*)

Honorary Meetings Secretary, Mrs J. Robertson (née Martin)

Back issues of Watsonia are handled by Messrs Wm Dawson & Sons Limited, Cannon House, Folkestone, Kent, to whom orders for all issues prior to Volume 15 part 1 should be sent.

Recent issues (Vol. 15 part 1 onwards) are available from the Hon. Treasurer of the B.S.B.I., 68 Outwoods Road, Loughborough, Leicestershire.

Watsonia, **15**, 177–181 (1985)

Presidential Address, 1984

J. F. M. CANNON

SEABALLS AND LAKEBALLS – AN OLD MEDITERRANEAN THEME WITH A NEW IRISH VARIATION

Successive Presidents of the B.S.B.I. have repeatedly laid stress on the fruitful cooperation between amateurs and professionals that has been such an important feature of the Society for many years past. Most notably in recent years, Mr R. W. David at the 1980 Annual General Meeting in Cambridge gave a most elegant, urbane and wide-ranging review under the title 'Gentlemen and Players'. In my address this morning, I shall not attempt to emulate his approach, but I shall try to illustrate an aspect of the relationship between amateurism and professionalism that has not attracted much attention. In so doing, I pay my tribute to this twofold dependency which contributes so much to the on-going vitality of the Society. The high standard of expertise achieved by some amateurs is fully worthy of comparison with the activities of professionals and, as such, has not infrequently been a source of comment both in our own field and in related areas of Natural History. We hear much less about the 'amateur' activities of professional botanists. By these I do not, of course, imply the perjorative sense in which the word amateur is so often used today, but rather the true meaning of the word conveying involvement with an activity solely for the pleasure it engenders and without thought of financial or other advantage. Activities undertaken solely because they are worthwhile and enjoyable are always especially pleasing; and botanizing for fun can help the sometimes jaded professional to relive the simple pleasures of earlier stages in a botanical life not least through holiday activities which can make the proverbial busman's holiday look recklessly wide-ranging by comparison. As with the 'professional amateurs', we are fortunate that our Society fosters many opportunities for a genuinely amateur love of botany amongst our professional membership. My concern with seaballs has been very much an 'amateur' interest, and may perhaps illustrate my general theme, not least through the homely nature of the only equipment involved in the experimental phase of the investigation.

My curiosity was aroused more than 30 years ago when, as a recently appointed member of the British Museum staff, I had to deal with an enquiry from a lady who had been on holiday to the Mediterranean. She had found a strange fibrous ball on the beach, about 8 cm in diameter and so regular as to appear man-made. More experienced colleagues at once recognized it as a *Posidonia* ball which, in those days, were quite often the subject of public enquiries. They do not seem to engage the attention of today's holiday-makers so frequently; perhaps the natural wonders of the Mediterranean now seem commonplace in this era of mass-produced and packaged travel. In due course, I visited the Mediterranean myself and was delighted to find large numbers of these strange objects cast up on the beach. Conventional wisdom refers to the balls as being formed by wave action from the fibrous remains of *Posidonia* leaves, which sounds an easy explanation until you actually wonder how it happens – a topic to which I shall return later. *Posidonia oceanica* is one of the very few truly marine flowering plants and is related to the *Zostera* species that are familiar to most British field botanists. In the Mediterranean, *Posidonia* forms wide 'meadows' in the shallow water adjacent to the gently sloping sandy beaches. The only real way to gain an impression of these communities is through the use of a diving mask and snorkel, and there can be few more relaxing ways of botanizing than floating gently over a *Posidonia* bed and observing the plants and numerous small animals that shelter in its often quite dense growth. The growth habit of *Posidonia* is reminiscent of a miniature rhizomatous *Iris*, and the fibres from which the balls are made are gradually released from the eroding leaves and leaf bases. Elsie Parry, an American author of a semi-popular article on seaballs wrote: "The Mediterranean Sea has long been the producer of fascinating wonders. The seaball is one of its 'Grade B' productions that has been appearing since ancient times. Greek and Roman writers mentioned 'bodies' that had been 'abandoned' by the sea. Galen and Aristotle wrote about using the ashes of seaballs as a cure for scrofula, and in 1837 Germain de Saint-Pierre reported that hunters in Provence used the balls to wad their guns. Today, in districts where they are plentiful, seaballs are used commercially in the manufacture of paper and mattresses" (Parry 1956). Although the balls sometimes occur in vast numbers, I am not aware of any current commercial exploitation and suspect that, in these days of extreme industrialization, the economic utilization of the balls may be a thing of the past.

My concern with seaballs gradually led me to take a somewhat casual interest in the wider aspects of ball formation in the plant kingdom, and in this I have been greatly assisted by my colleagues with specialist knowledge of the groups concerned. Some of the strangest instances of ball formation are found in the lower cryptogamic groups, such as the green and red algae and the mosses. Unlike the *Posidonia* balls, which are composed of dead plant detritus, the algal and moss balls consist of living plants and while, like *Posidonia*, they owe their origin to purely physical factors, their maintenance and growth is partly a result of the activities of the living plant. The best known of these are formed in both sea and freshwater by species of the green filamentous alga *Cladophora*, and in these and similar cases the balls are known as aegagropilous forms of the normal species. On occasions they can occur in great abundance and may even attract sensational headlines in the media, as when in 1950 an article appeared in the *Illustrated London News* entitled 'A beach ball mystery at Torbay'. On this occasion a 10 ft wide belt at least a mile long, containing many millions of balls, was formed on the beach (Newton 1950). A similar occurrence was reported as an extensive deposit of 'sea manure' in 1903 at Lynn Beach in Massachusetts. Cladophoras have also attracted attention through their tendency to form balls in fresh water. These have received special notice in Japan, where a particular lake – Lake Akan, Hokkaido – has even been designated as a 'Special Natural Monument of Japan', and the balls have received the ultimate accolade – depiction on a postage stamp. The balls are formed by water movements from growing filaments and gradually become larger, though the annual incremental growth is often very slow, being as little as 5–10 mm in large balls which have been compared to footballs in size. In section, the balls often show indistinct concentric rings, which may be analogous to the annual growth rings of trees, although there does not seem to be any very firm basis for this interpretation. The centre of old balls frequently decays to a greater or lesser extent and, since the filaments that form the walls of the *Cladophora* balls are living, they photosynthesize and respire like any other chlorophyll-containing plant tissue. As a result, their density may be altered by the release of gases from these metabolic activities, and consequently the balls rise or fall in the water in patterns that may be related to the diurnal physiological activity of the cells. It may be this factor that has specially contributed to the popular interest of the Japanese and others in the lakeball phenomenon, and those in Lake Akan were apparently venerated by the local tribe in times past. Lakeballs were first recorded as long ago as 1588, when they were referred to by Öle Worm, alias Wormius, a Danish doctor of medicine, who called them "pilla aquatica". The first record in Britain appears to come from the letters of Thomas Knowlton, a distinguished gardener and plantsman who in the earlier part of the 18th century was corresponding with various men of science and learning.

Some species of red seaweeds lay down calcareous deposits and can contribute to reef formation somewhat in the manner of corals. Surprisingly, calcified algal protruberances can become detached and can then go on growing as calcareous algal balls. The continued growth of the whole ball is, of course, dependent on continued movement by waves and tidal currents, so that all aspects of the balls are more or less equally exposed to sunlight. In some places such as Brittany, Cornwall and parts of the western coast of Ireland, these balls are so numerous as to form beds or bands known as Maërl. The Maërl beds of Brittany have been exploited by dredging as a commercial source of lime for agricultural purposes (Blunden *et al.* 1975). The whole topic of unattached seaweeds has been ably reviewed by Norton & Mathieson (1983).

Ball formation by semi-aquatic mosses has also been quite frequently recorded, as in a recent paper by Deguchi & Inoue (1982), in which balls formed by mosses of the genera *Blindia* and *Drepanocladus* were noted from lakes in Tierra del Fuego and southern Chile. As with the algae, the balls seem to have functioned as living organisms.

Digressing briefly to consider similar structures and functions in terrestrial plants, we may recall that moss balls on land have been described from a wide range of habitats, from forest floors, through sandy and gravelly barren ground to the surface of glaciers. In a recently described example from wetland forest near Amstelveen in the Province of North Holland, Wiegers (1984) discovered that the motive power that kept balls, composed of the mosses *Dicranum scoparium* and *Mnium hornum*, in motion was the eager beak movements of foraging pheasants searching for food on the forest floor. Balls composed of *Leucobryum glaucum* are not infrequently seen in places where the moss can grow relatively undisturbed by human activities. The occurrence of moss balls on ablating glacier ice is sufficiently well-known to have achieved a vernacular name – 'glacier mice', no doubt a reference to their round, furry appearance. In this case, the general instability of the habitat, coupled with the rigorous climate, tends to maintain mobility and, at the same time, promotes the colonization of newly opened habitats (Richardson 1981). Somewhat similar life forms are known in lichens (Weber 1977) where they are sometimes referred to as 'vagrants'. Examples are often found in the genera *Aspilicia* and *Chrondropsis* in high, open, windy areas in Asia and the manna which the Bible records as saving the starving Israelites in the desert has been ascribed to a similar source. Under moist conditions the lichens may open out, curling into a ball again with the onset of arid conditions. This may be a means of dispersal and as such is reminiscent of the tumbleweeds, a life form that includes plants as various as a *Selaginella* and a heterogeneous range of flowering plants of open habitats. These species grow under desert-like conditions, and during droughts roll into balls, which may become detached and roll around in the wind. In the course of this movement, seeds may be dispersed and eventually, with the return of moist conditions, the plants open out and may become reattached in some favourable situation for further growth. Such plants are sometimes seen in tourist and curio shops under names such as Rose of Jericho or Resurrection Plant.

This is perhaps enough general background and I must now return to my major theme of *Posidonia* balls. When explaining to enquirers how the balls are formed, I have frequently found myself sharing their incredulity that the simple physical forces of wave and current, acting on a supply of plant fibres, could result in such remarkably uniform objects, so as to cause their finders to believe them to be man-made. As a starting point for understanding the processes involved, we should remember that animal and plant fibres which to us seem smooth, are actually quite rough at the microscopical level, with minute scales. Without these, wool from animals and flax and cotton from plants could not be arranged in an orderly manner during the process of spinning, and then remain twisted and adhering together to form usable threads. Likewise, and perhaps here the parallel is closer to *Posidonia*, wet wool can be manually compacted in such a way as to produce a stable fabric – felt. But at the spinner's wheel or spindle we are still a long way from explaining what happens at the bottom of the sea.

The nagging doubt as to how the balls were formed remained until a few years ago, when I noticed that our domestic washing machine (Hotpoint Automatic De Luxe 1972 – a 'top loader') was producing small objects, quite reminiscent of *Posidonia* balls, from the miscellaneous textile fibres that became detached from clothing in the wash. Most, if not all, washing machines have a lint-trap to collect these fibres and the machine in question had a trap in the form of an oscillating plastic sieve, 21.5 cm in diameter and 3 cm deep. The sieve, which has numerous fine drainage holes, is situated on the top of the main agitator, and oscillates in the horizontal plane through c. 90° at a rate of 80 cycles per minute. Water from the main washing drum is circulated through a spout above the sieve while the main washing programme is in operation, so that fibres which might otherwise clog the machine are filtered from the water. Here at last was the moment of breakthrough! If the washing machine could make incipient balls from clothes fibres, could it also make an artificial *Posidonia* ball from *Posidonia* fibres? With some trepidation we decided to carry out some experiments, fearful lest the bowels of the machine were at risk from this unaccustomed diet. Fortunately, the machine would operate during the washing phase with the lid open, so it was possible to observe what took place. I am glad to be able to record that it survived the ordeal to give further years of faithful service.

A ball from Giens in southern France was carefully broken down by hand to its constituent fibres. These were placed in the main drum and, when operations were started, gradually made their appearance in the filter tray. Soon some of the fibres started clumping together in loose, soggy masses of about 1–2×0.5 cm. These initials were very fragile so that, if two or more came into contact, disintegration often occurred, although rarely, amalgamation took place. The rate of availability of fibres is an important factor. This is not a simple process of accretion, as when a snowball is rolled along the ground, and our observations showed that if fibres are too abundant, ball formation tends not to occur, as the numerous initials interact and mutually disrupt at early stages. When a ball has grown to the initial stage, it is still very delicate and loosely constructed. It is now essential for the second phase of ball formation to come into play. The ball is now gradually consolidated towards the firm consistency with which we are familiar. This results from backwards and forwards rolling and, for this to occur, the nature of the substrate is important so that, when the water changes direction, the friction between the ball and the sandy bottom results in a rolling rather than a skidding motion. In our experimental model, the holes on the bottom of the sieve acted in a manner analogous to the sand grains on the sea bed. Under these experimental conditions, three washing cycles of ten minutes produced a reasonably compacted ball of 5.0×3.5 cm. While the experiment demonstrated some of the factors involved in ball formation, no real light is shed on the time involved under actual seabed conditions (Cannon 1979).

So much then for the classic Mediterranean theme; what about the new Irish variation? Last year when Mr A. O. Chater, Dr S. M. Walters and Prof. D. A. Webb were walking on the Inch sand spit which projects southwards across Dingle Bay in Kerry, some 35 km from its seaward end, they encountered a fibrous structure remarkably similar to a *Posidonia* ball. So far, efforts to determine its origin and composition have not been very successful. I am indebted to Dr Paula Rudall of the Jodrell Laboratory of the Royal Botanic Gardens, Kew, who kindly made an anatomical examination of the ball's fibres. She reports that they are the central vascular portions of roots, but with the cortex and epidermis lacking. They are most likely from a Monocotyledon, as they are polyarch with no secondary growth, and have a multilayered pericycle which occurs in many Monocotyledons such as grasses. But as primary root structures do not vary very much, and published data and reference materials are not very extensive, a more detailed identification was not possible. Where did it come from? Correspondence with Dr E. C. Nelson of the National Botanic Gardens, Glasnevin, Dublin, who has made extensive studies of drift seeds brought by the Gulf Stream, failed to produce evidence of any comparable occurrences. In his opinion, a fibrous structure of this kind would be unlikely to remain afloat for the fifteen or more months needed to cross the Atlantic from the Caribbean, even supposing it had a dry terrestrial origin. So we are left with another, albeit minor, enigma in the flora of our islands. Members are invited to keep their eyes open while walking on Irish and British beaches. Was the Chater/Walters/Webb ball a unique occurrence? Clearly much remains to be discovered about plant fibre balls. For instance, in the Kew Museum there are balls formed "from larch leaves felted together by the agitation of water, taken from the bottom of lakes of Shropshire and in Bagshot Park". In the British Isles we cannot hope to rival the prodigious ball productivity of the Mediterranean, but there may yet be matters of interest to discover in this somewhat unusual field of Natural History.

REFERENCES

Blunden, G., Binns, W. W. & Perks, F. (1975). Commercial collection and utilisation of Maërl. *Econ. Bot.*, **29**: 140–145.

Cannon, J. F. M. (1979). An experimental investigation of *Posidonia* balls. *Aquat. Bot.*, **6**: 407–410.

Deguchi, H. & Inoue, H. (1982). Lake moss-balls found in Tierra del Fuego and Brunswick Peninsula, southern South America. *Bull. natn. Sci. Mus., Tokyo*, Ser. B (Botany), **8**: 145–150.

Kurogi, M. (1980). Lake ball 'Marimo' in Lake Akan. *Jap. J. Phycol.*, **28**: 168–169.

Newton, L. M. (1950). A beach ball mystery at Torbay. *Illust. Lond. News*, **216**: 98.

Norton, T. A. & Mathieson, A. C. (1983). The biology of unattached seaweeds, in Round, F. E. & Chapman, D. J., eds. *Progress in Phycological Research*, **2**: 333–386. New York.

Parry, E. A. (1956). Beachcomber's treasure – a sea ball. *Nat. Hist., N.Y.*, **65**: 496–497.

Richardson, D. H. S. (1981). *The biology of mosses.* Oxford.

Weber, W. A. (1977). Environmental modification and lichen taxonomy, in Seaward, M. R. D., ed. *Lichen ecology*, pp. 9–29. London.

Wiegers, J. (1984). Observations on the origin of 'moss balls' in a Dutch wetland forest. *Beitr. Bio. Pfl.*, **58**: 449–454.

NOTE ADDED IN PROOF

Since this address was given, my wife and I have had the opportunity of visiting the Inch sand spit in Dingle Bay, where Chater, Walters and Webb found the mystery seaball. We were able to find a considerable number of the balls and to reach the conclusion that their major constituent was fibrous material from *Ammophila arenaria* roots, as had been suggested might be the case by Dr T.

G. F. Curtis (after the address was presented for a second time at the B.S.B.I. Irish Region Annual General Meeting on Saturday 8th September 1984). The question still remains, however, as to whether this locality is the only site in the British Isles where seaballs are produced from this apparently abundant raw material.

Watsonia, **15**, 183–209 (1985)

Taxonomy of *Atriplex* species indigenous to the British Isles

P. M. TASCHEREAU*

Department of Botany, University of Manchester

ABSTRACT

A biosystematic study of the genus *Atriplex* (Chenopodiaceae) based on field, culture, experimental hybridization, herbarium and cytological work delineates the taxa of this genus indigenous to the British Isles. Detailed morphological descriptions are given and distribution maps and illustrations provided for *A. prostrata* Boucher ex DC., *A. glabriuscula* Edmondston, *A. longipes* Drejer, *A. praecox* Hülphers, *A. littoralis* L., *A. patula* L., and *A. laciniata* L. The habitats and reproductive biology of the species are discussed and the chromosome numbers reported. Hybrid derivatives between *A. longipes* and *A. glabriuscula* and between *A. longipes* and *A. prostrata* are common in many areas of the coast. The following hybrids are also reported: *A. glabriuscula* × *A. praecox*, *A. glabriuscula* × *A. prostrata*, *A. littoralis* × *A. prostrata*, and *A. littoralis* × *A. patula*.

INTRODUCTION

The most recent treatment of *Atriplex* occurring in the British Isles is that of Aellen (1964) in *Flora Europaea*. According to Aellen the following species are native: *A. laciniata* L., *A. patula* L., *A. littoralis* L., *A. prostrata* Boucher ex DC. (*A. hastata*), *A. glabriuscula* Edmonston and *A. longipes* Drejer.

Atriplex laciniata is placed in section *Sclerocalymma* Aschers., and the remaining species in section *Teutliopsis* Dum. Within this section *A. prostrata*, *A. glabriuscula* and *A. longipes* form a recognizable unit, the *A. prostrata* group or *Hastata* complex.

The taxonomic problems in British *Atriplex* species have been concerned with the members of section *Teutliopsis* and in particular with the *A. prostrata* group. In section *Teutliopsis*, the number of species recognized in British floristic works has varied from one in Bentham & Hooker (1896) to nine in Babington (1841). Druce (1928) recognized 21 native taxa of which six were treated by him as species and one was considered a hybrid. The considerable variation within the *A. prostrata* group is reflected in the taxonomic treatment it has received from British authors. In 1860, C. C. Babington wrote that G. Bentham believed *A. glabriuscula* to be indistinguishable from *A. prostrata* (A. M. Babington 1897). This difference of opinion resulted in different treatments of these plants in two important British floras – that of Babington (1843) and of Bentham & Hooker (1896). Hulme (1957) did not distinguish between the coastal forms of the *A. prostrata* group, referring to them as "*hastata-glabriuscula*". Tutin (1962), while treating *A. glabriuscula* as a species distinct from *A. prostrata*, added the remark that *A. glabriuscula* is "probably best regarded as a subspecies of it".

Until recently only *A. prostrata* and *A. glabriuscula* were recognized as occurring in Britain. Hulme (Aellen 1964) mentioned *A. longipes*, which was said to be "widespread in the British Isles", but other authorities (Gustafsson 1972) doubted its presence here and no material was available for study. Jones (1975) observed plants resembling *A. longipes* in a few localities in Britain and she suggested that this taxon was present here. In 1977, I reported the presence of *A. praecox* Hülphers in the British Isles and confirmed the presence of *A. longipes* (Taschereau 1977). Taxonomic ranking within the *A. prostrata* group, previously concerned only with *A. glabriuscula*, must now consider these two additional members of the group.

---

*Present address: *Institute for Resource and Environmental Studies, Dalhousie University, Halifax, Nova Scotia, Canada, B3H 3E2*

Although many authors have written about *Atriplex*, relatively few have contributed much to our understanding. Moss & Wilmott (1914) provided a well-illustrated and helpful monographic account of the *Atriplex* species occurring in Britain. Aellen (1960) dealt with the taxonomy, distribution, ecology and economic uses of European *Atriplex*, and in 1964 he provided a revised account of their taxonomy and distribution.

Biosystematic studies have been extremely important in elucidating the taxonomy of species in section *Teutliopsis*: Turesson (1922a, 1922b, 1925), in a series of pioneer studies, demonstrated the value of extensive cultivation experiments and experimental hybridization in understanding the complexities of this group. Hulme (1957, 1958) produced the first controlled experimental hybrids in *Atriplex* thereby demonstrating the feasibility of this approach to the study of the genus. Her work was of key importance in understanding the taxonomy of section *Teutliopsis* in North America as well as in Britain. Hulme's experimental findings supported the taxonomic separation of the tetraploid *A. patula* from the diploids *A. littoralis* and *A. prostrata* and the maintenance of these taxa at the level of species. Bentham & Hooker (1896) had united them as intergrading variants of *A. patula*. Although by 1957 most British and European authors were treating all three taxa as separate species, this was not the case in North America. Since Gray (1868), North American taxonomists had regarded the members of section *Teutliopsis* including *A. prostrata* and *A. littoralis* to be intergrading varieties of *A. patula*, and they continued to do so until convinced otherwise by Hulme's data and subsequent studies (Taschereau 1972). (The confusion resulting from this traditional taxonomic treatment is still evident in ecological papers from North America in which *A. patula* is referred to as a halophyte and a component of salt marsh communities. In North America, as in Britain and elsewhere, *A. patula* is a ruderal and colonizer of disturbed soil, relatively salt tolerant but not a halophyte and never a component of salt marsh communities.)

Minor contributions to the experimental taxonomy of section *Teutliopsis* were made by van der Meijden (1970) in the Netherlands, and by Jones (1975a, 1975b) in Britain. Neither author did extensive cultivation experiments nor attempted to make hybrids.

The most extensive and important biosystematic studies in *Atriplex* are those by Gustafsson (1972, 1973a, 1973b, 1974, 1976) of the *A. prostrata* group in Scandinavia. They provide a foundation for understanding the group as it occurs in the British Isles. Without Gustafsson's many experimental hybrid specimens for reference, accurate identification of the hybrid derivatives that comprise so much of the British coastal *Atriplex* flora would have been impossible.

MATERIALS AND METHODS

The present work is based on a four-year study of the genus in the field, laboratory and botanic garden.

FIELD STUDIES

Great Britain

Areas within each of the major plant regions of Britain (Heath & Scott 1974) were examined at least once between 1974 and 1978. 75 sites covering 27 vice-counties were visited. The areas included 61 coastal and estuarine habitat sites, three inland salt marshes and eleven inland sites on disturbed ground. The location of these sites is given in Fig. 1.

Samples were taken from 255 populations and collections made comprising approximately 1,270 pressed herbarium specimens. All but three of my locality records cited in this paper are supported by voucher specimens filed in **MANCH**.

In 1977, a comprehensive survey of the *Atriplex* taxa on the coasts of the British Isles was undertaken through the Botanical Society of the British Isles in cooperation with the Biological Records Centre, Monks Wood. The 251 herbarium specimens collected by the participants and 80 data cards were sent to me for identification and checking. Data were obtained from 36 vice-counties representing all coastal regions except south-western England and the coasts of Ireland. The areas from which specimens were received are shown in Fig. 1.

Sweden

Three coastal localities in the province of Skåne in southern Sweden were examined with M. Gustafsson in 1975: Bunkeflo and Skanör Harbour south of Malmö, and Torekov near Ängelholm

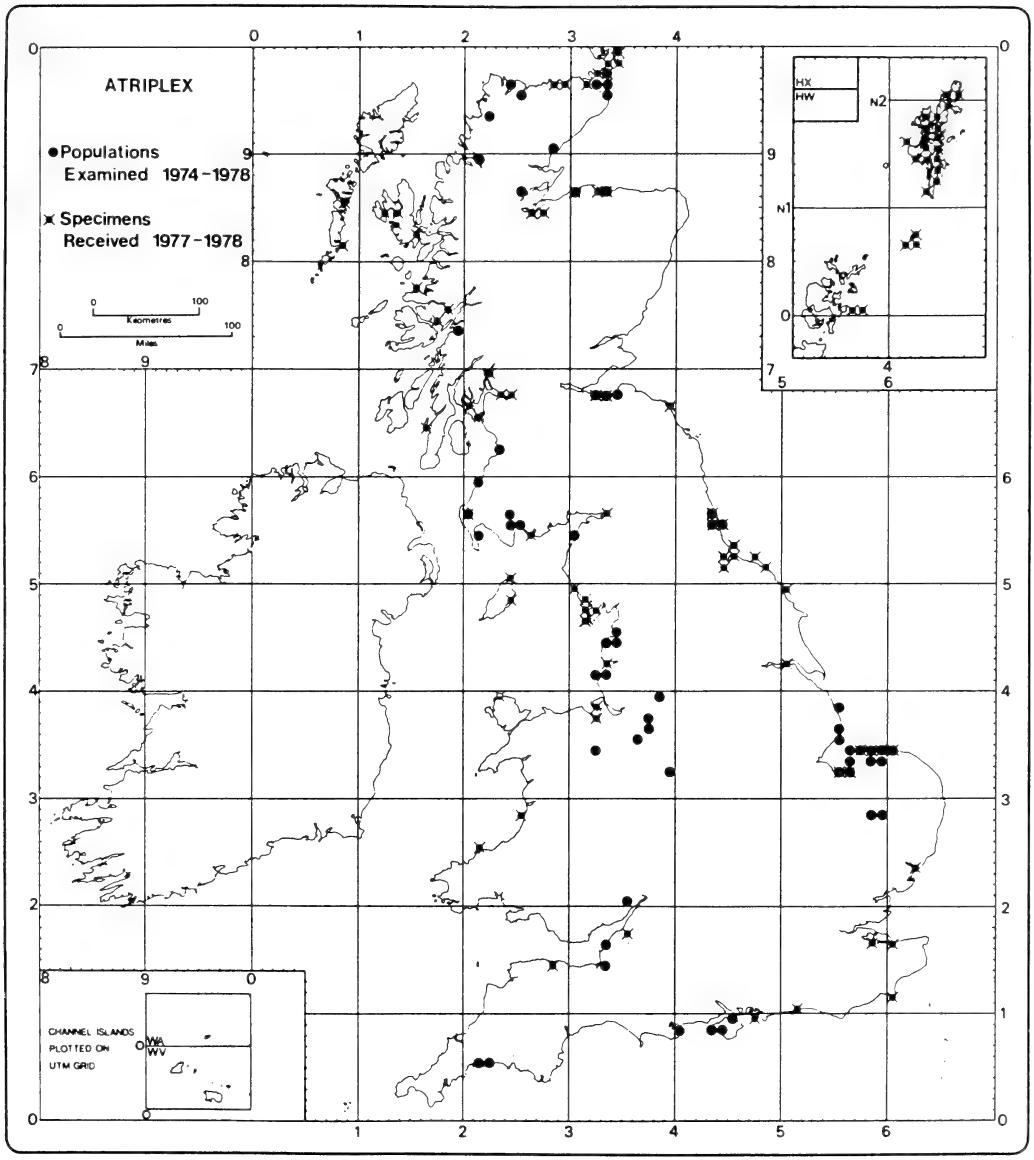


FIGURE 1. Localities from which *Atriplex* plants were examined.

on the south-western coast. The Torekov site was studied by Turesson (1925) in his work on the genus *Atriplex*, and all the localities visited provided material for the *Atriplex* investigations by Gustafsson (1976).

In 1976, three localities were examined on the coasts of the Baltic Sea: Kalmar on the mainland, Stora Rör and Ottenby on the island of Öland. Ottenby is the restricted type locality of *Atriplex hastata* L. (Stearn 1973). In total, six Swedish sites were examined and three populations were sampled, the taxa comprising five species and four hybrids.

CULTIVATION

Large numbers of plants were cultivated to study regional variation and phenotypic plasticity. Plants were also cultivated to confirm identification, to facilitate observations on reproductive biology, to make artificial hybrids and to observe segregation in natural and artificial hybrid progeny. From 1974 to 1978, approximately 2,650 plants were cultivated either in the greenhouse or in outdoor plots in the botanic garden. Of these, about 1,280 were grown to maturity. These included 27 taxa comprising representatives of all the four European sections of the genus. For reference and study, 380 specimens of pressed plants consisting of stems, leaves, bracteoles and fruit were prepared from the cultivated material, as well as 75 specimens consisting only of bracteoles and fruit.

Seeds were sown in trays of John Innes Seed Compost in the autumn and placed in an unheated greenhouse over winter. In this way the dormancy encountered in several species was overcome. The seedlings were later transferred to individual pots containing John Innes Potting Compost. Dormancy in almost all seeds could be overcome by placing the moistened seeds in a controlled cycling environment (Ignaciuk & Lee 1980) where they were exposed to 9 hours dark at 10°C and 15 hours light at 30°C. Germination then occurred within two weeks. In a few cases, however, seeds in the controlled cycling environment germinated only after the seed coat was also removed.

CYTOLOGY

The chromosomes are small (2–3 μm), metacentric to submetacentric, and morphologically similar. The basic number in the genus is $x=9$. Endomitosis, the formation of cells containing multiples of the normal somatic number, is a phenomenon encountered in *Atriplex* root-tips, and one that complicates chromosome counting. Diploid, tetraploid and octoploid cells are commonly present in the same root-tip preparation. Polyploid cells increase in number along the root-tip. They can be largely avoided in cytological preparations by utilizing only a minute section of the root behind the root-cap.

Root-tips obtained from vigorous young plants cultivated in pots in the greenhouse were pretreated overnight in 0.2 mM solution of 8-hydroxyquinoline at 5°C then fixed in absolute alcohol-glacial acetic acid (3:1) for 24 hours. The material was then transferred to 70% alcohol and stored in the deep freeze until use. The tips were hydrolysed in 1N HCl for 9 minutes at 60°C then stained in Feulgen for 2 hours. The excised tip was tapped and squashed in lacto-propionic orcein.

Meiotic preparations were made by fixing very young buds in a mixture of absolute alcohol, chloroform and glacial acetic acid (6:3:1) for 24 hours in the deep freeze. The fixed buds were transferred to 70% alcohol before use then dissected out in 45% lacto-propionic acid and squashed in lacto-propionic orcein.

HERBARIUM

Descriptions and other taxonomic data presented in this study are based almost entirely on specimens I collected between 1974–1978 or collections made by others during that period and sent to me. Herbarium studies were used primarily to supplement and confirm these data and to establish the extent of variation within taxa from widely separate geographic regions. My distribution records of *A. patula*, *A. prostrata*, *A. littoralis* and *A. laciniata* are supplemented by data provided by the Biological Records Centre. Additional distribution records of *A. glabriuscula* and *A. praecox* are based only on herbarium specimens I identified.

Material from the following herbaria was studied: **ABD**, **ANK**, **BM**, **C**, **CGE**, **DBN**, **E**, **K**, **LD**, **LIV**, **LIVU**, **MANCH**, **NMW**, **OXF**, **SLBI**, **TCD** (abbreviations according to Kent & Allen (1984) and Holmgren *et al.* (1981)). Herb. B. Hulme at **LIV** was also examined.

Specimens are not cited in this paper. I have, however, annotated the entire holdings of the following major British and Irish herbaria: **ABD**, **CGE**, **DBN**, **E**, **LIV**, **LIVU**, **TCD**. Also, approximately half of the large holdings of **NMW** have been annotated by me.

DIAGNOSTIC CHARACTERS

The diagnostic characters used in *Atriplex* identification differ from those used in other chenopod genera. The inflorescence provides few characters, and the flowers virtually none. Even seed surface sculpturing, a character found so useful for separating closely related species of *Chenopodium* (Cole 1961), has so far not proved helpful in *Atriplex*.

Within a species, the leaf outline can vary from one biotype to another in the same habitat and from one node to the next on the same plant. Within a species, colour, vestiture and habit can vary due to genetic difference or because of environmental factors. Leaf colour outline and vestiture can also change with the maturity of the plant. Younger leaves or those remaining on the plant at maturity can differ greatly from mature leaves or the earlier-formed leaves that may have dropped off the plant by maturity.

Most characters are to some extent variable. In some cases, the phenotypic plasticity is such that particular environmental factors can cause plants of one species to resemble the phenotype of another, genetically different species.

The most important diagnostic characters are those of the lower principal leaves and of the fruiting unit. The latter consists of the seed with surrounding pericarp and the pair of bracteoles within which they are enclosed. Separation of species in section *Teutliopsis* depends essentially on the existence of a consistent correlation between the characters of the lower leaves and those of the fruiting unit.

Some species have a restricted range in Great Britain and some occupy relatively specific habitats. Information about the habitat and locality is particularly useful in this group.

Special terms used in the key and descriptions are illustrated in Fig. 2 and explained along with the major diagnostic characters below.

HABIT

Atriplex may be erect with branches ascending or outspreading, or prostrate (decumbent or procumbent). My experiments and those of Turesson (1919) indicate that environment, particularly light, nutrient and moisture, has a considerable effect on the habit of some species. In several species two variants exist: a hereditary prostrate kind and a modificatory prostrate kind. In the latter, intense light induces a plagiotropic response in a normally erect plant; and in the former, shading causes the branches to turn upwards (Turesson 1919).

Though variable in some species, the habit is often distinctive. *A. littoralis* in Britain is consistently erect. *A. glabriuscula* is characteristically procumbent on exposed beaches, becoming decumbent to weakly erect when crowded at the landward margin of the beach, but also possessing a less common erect variant. *A. patula*, commonly erect though often spindly and falling over, has hereditary and modificatory prostrate variants. *A. prostrata* has erect and prostrate kinds.

LEAVES

Lower Principal. The lower principal leaves are the earlier-formed leaves on the central axis in the middle to lower part of the plant, at approximately nodes 4 to 8 up from the base, between flowering and the development of mature fruit. They often differ considerably in size and form from the later-developing upper leaves and they frequently drop off before the bracteoles and seed are fully mature. The lower leaves on *A. longipes*, for example, are elongate-triangular with basal lobes while the upper leaves that develop on older specimens are lanceolate to linear and frequently entire. By the time the plants reach maturity, the only leaves that remain on them may be the lanceolate to linear ones.

Outline. The leaf outline, although extremely variable within some species, is an essential diagnostic character. The outline of the lower principal leaves is less variable and it is these that are taxonomically significant.

Base. The leaf base angle of the lower principal leaves, cautiously employed, can provide a useful secondary character. It is too variable to be used alone to separate *A. glabriuscula* from *A. prostrata* but other species have a characteristic base. In *A. patula* and *A. praecox*, for example, the leaf base is cuneate and in *A. longipes* it is cuneate to obtuse. The leaf base often serves as a useful character for detecting hybrids between species with truncate leaves and those with cuneate leaves. Between the upper and lower leaves on the same plant, the leaf base angle is often very different, and in some individuals it varies greatly even from one node to the next.

Succulence. Leaf succulence has little diagnostic value, although some individuals of *A. glabriuscula* may have extremely succulent leaves. Specimens of the hybrid *A. littoralis* × *A. prostrata* are usually extremely succulent, perhaps as a result of positive heterosis.

Colour. Betacyanins (Dreiding 1961) are responsible for the red colour in *Atriplex*. As a taxonomic

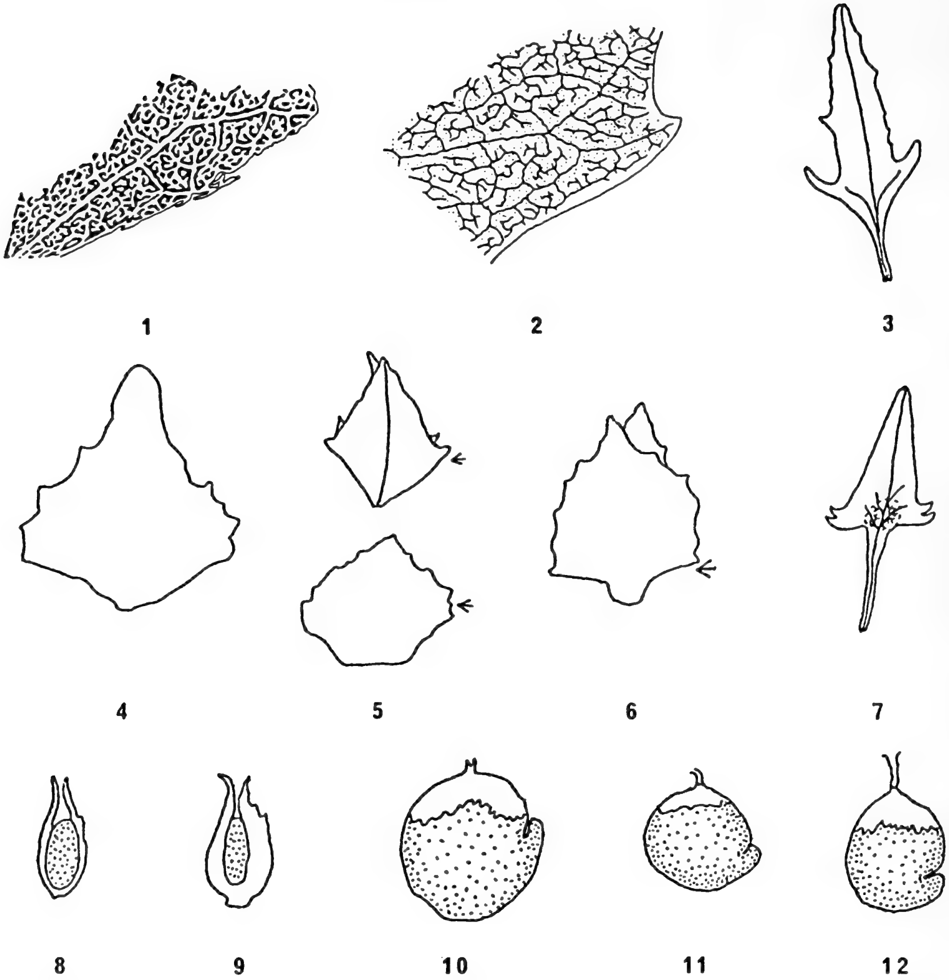


FIGURE 2. Diagnostic characters used in *Atriplex*.
1. Kranztypus leaf venation (section *Sclerocalymma*); 2. Normal dicotyledonous leaf venation (section *Teutliopsis*); 3. Forward-curving basal lobes; 4. Lingulate apex; 5. Bracteole margins united up to the middle (arrow); 6. Bracteole margins united only at the base (arrow); 7. Stalked bracteole; 8. Bracteoles thin or evenly-thickened; 9. Bracteoles spongy-thick from the middle to the base; 10. Seed radicle strongly up-pointing; 11. Seed radicle obliquely up-pointing; 12. Seed radicle out-pointing.

character colour is of secondary importance. The red colour in some individuals may be the result of a genetic difference, but the development of red may depend largely on environmental factors. *A. praecox* in Britain is characteristically red but in *A. glabriuscula*, reddish and entirely green plants commonly occur together in the same population. *A. littoralis* may be green or reddish and in *A. patula*, a species which is usually entirely green, reddish strains occur. The leaves of *A. longipes* frequently turn bright yellow at maturity but so do those of some of its hybrids with *A. prostrata*.

Vestiture. Young *Atriplex* leaves are covered with stalked, oblong, fluid-filled vesicular hairs. These, as the leaf matures, dry and form a scaly or mealy surface. As a taxonomic character, the density of the scales and their distribution on the leaf surface has limited usefulness. For example, the abundant mealiness on the leaves of some coastal species gives them a distinctive whitish appearance. *A. patula*, by contrast, has only a sparse, hardly discernible covering of fine mealy particles on the younger leaves.

Venation. Leaf venation in section *Teutliopsis* consists of the normal dicotyledonous type. Immature and densely lepidote specimens in section *Teutliopsis* can be immediately distinguished from *A. laciniata*, the only native species not in section *Teutliopsis*, by the leaf venation. *A. laciniata* possesses the highly distinctive Kranztypus venation (Fig. 2). This becomes readily visible with a hand lens when the leaf is scraped with a knife-blade.

BRACTEOLES

The breacteoles provide some of the most useful diagnostic characters. Within many species, however, there can be considerable variation. The variation may be due to genetic differences between biotypes of the same species or differences in the environmental factors acting on the same biotypes. Once the limits of variation are known within a species, the bracteole characters can be usefully employed. The following characters should be observed:

Outline. In most species the outline is either triangular, rhombic, ovate or some combination of these shapes.

Apex. In most species, the apex is usually either acute, acuminate, lingulate or produced to a thin foliose tip.

Base. In most species, the base is truncate, obtuse, or cuneate. The base, especially of bracteoles occurring in the axils of leaves or branches, should be examined for the presence of a stalk, a variable but important character whose presence is usually essential for the identification of hybrids involving *A. longipes*.

Margin. How far the bracteole margins are united up from the base is a major diagnostic character. The presence or absence of lateral angles is important. The degree to which the lateral angles are developed, whether the development is unilateral or bilateral, and whether the lateral angles are rounded or pointed are important characters. The degree of toothing and the position of the teeth are also significant.

Dorsal Surface. The dorsal surface is described as smooth, muricate or tuberculate, strongly reticulate-veined, 1-veined or obscurely-veined. Both smooth and tuberculate individuals may occur within one species, and the degree to which the veins are prominent varies within individuals of the same taxon, but once these limitations are known, the characters can be usefully employed.

Inner Surface. A layer of distinctive, brown or silvery-brown, spongy tissue of large air-filled parenchyma lines the inner surface of the bracteoles of certain species. Within a single taxon, this tissue may be undeveloped, developed only at the base, or developed over the entire surface. In *A. patula*, for example, it is never present, but it typically occurs in members of the *A. prostrata* group.

Substance. The bracteoles are described as membranous, herbaceous or spongy. Membranous bracteoles, such as often occur in *A. praecox* are so thin that the fruit, not merely its outline, can be seen within them. The bracteoles of *A. glabriuscula*, for example, are spongy, particularly in the basal portions. This spongy character is especially useful for distinguishing hybrids between *A. glabriuscula* and species that have membranous or herbaceous bracteoles.

SEEDS

The types of seeds present, their size, shape and position within the pericarp, provide important diagnostic criteria.

Dimorphism. On the same plant, two distinct seed types may occur: a brown type and a black type. The brown seeds are reddish to dark brown, usually larger than the black, flattened and disc-shaped, have a radicle that is distinctly produced, have a dull or pebbled-glossy surface with the radicle region often strongly striate-pebbled, and possess a softer outer coat. The black seeds in most species are generally smaller than the brown, are biconvex, have a radicle that is scarcely produced, have a smooth-glossy surface and possess a harder outer coat.

In some individuals, these morphological distinctions in seed type are relatively constant, but most taxa have many individuals in which numerous morphologically intermediate seed types occur. The relative abundance of the two seed types within the individual has slight taxonomic significance because the ratio may differ within strains of the same species. This is particularly true of *A. patula* and *A. littoralis*. In these species it is common to find that one or the other seed type predominates within a particular strain of plants.

The distinctions in radicle position and direction discussed below, as well as differences in seed shape, are much more apparent in the larger, brown and intermediate types than in the smaller black types.

Radicle Position and Direction. The position of the seed radicle and its direction are important taxonomic characters. Surrounding the seed is a loosely or firmly attached membranous pericarp with the vestiges of the style situated at the top. The outline of the radicle becomes visible on the seed margin when the lower part of the pericarp is teased away. The radicle may emerge from the middle portion of the seed margin ('median') or from the base of the seed ('basal'). The radicle apex may be directed upwards towards the style vestiges ('up-pointing'), or outwards at a right angle to the style axis ('out-pointing'), or at an angle between these directions ('obliquely up-pointing').

KEY TO THE SPECIES

1. Leaf venation appearing (at ×12) as a conspicuous, dark green, reticulate pattern (Kranztypus) when the leaf surface is scraped with a sharp blade; bracteoles cartilaginous and hardened in the lower half; seed transversely elliptical, light brown .... 7. *A. laciniata*

1. Leaf venation appearing (at ×12) as the normal dicotyledonous type and not showing a dark green reticulate pattern when the leaf surface is scraped with a sharp blade; bracteoles herbaceous, membranous or spongy-inflated, not hardened in the lower half; seed ovate to orbicular, dark brown or black 2

2. Lower leaves linear or lanceolate 3

2. Lower leaves triangular or rhombic-ovate 4

3. The lower leaves linear without basal lobes; bracteoles ovate, thick, margins united only at the base, apices acute or lingulate and frequently reflexed at maturity. Coastal halophyte .... 5. *A. littoralis*

3. The lower leaves lanceolate with forward-curving basal lobes; bracteoles rhombic, thin, margins united almost to the middle, apices acute to acuminate and never reflexed at maturity. Non-halophytic inland and coastal weed of disturbed ground .... 6. *A. patula*

4. Lower leaves rhombic-ovate; mature plants small (mostly 8–10 cm high). Restricted to lower littoral zone of coastal beaches .... 4. *A. praecox*

4. Lower leaves triangular; mature plants larger (mostly more than 20 cm high). Occurring throughout the littoral zone of coastal beaches and inland 5

5. Bracteoles rhombic, margins united up to the middle, spongy-thick from the middle to the base; seed radicle strongly up-pointing. Coastal halophyte .... 2. *A. glabriuscula*

5. Bracteoles ovate or triangular, margins united only at the base, thin or evenly thickened; seed radicle out-pointing or obliquely up-pointing. Coastal and inland 6

6. Lower leaves deltoid-triangular, length less than twice the width, base truncate to subcordate (base angle more than 160°); axillary bracteoles infrequent, morphologically similar to terminal ones, thin or evenly thickened, none foliaceous; margins with pointed or rounded, weakly developed lateral angles; dorsal surface smooth or weakly veined towards the base; sessile. Coastal and inland in saline or weedy habitats .... 1. *A. prostrata*

6. Lower leaves narrowly triangular, length about twice the width, base cuneate (basal angle less than 150°); axillary bracteoles frequent, morphologically different from terminal ones, thin, at least some of them foliaceous; margins with pointed, strongly developed lateral angles; dorsal surface strongly reticulate-veined towards the base; stalked (stalks 5–25 mm long). Restricted to estuarine salt marshes in tall vegetation .... 3. *A. longipes*

DESCRIPTIONS

ATRIPLEX Section *TEUTLIOPSIS* Dumort., *Fl. Belg.*, p. 20 (1827).

Stems green with whitish, stramineous or red stripes. Venation normal dicotyledonous type. Flowers monoecious, the pistillate ones all bracteolate and lacking a perianth. Bracteoles united at the base or up to the middle at most, not becoming cartilaginous in fruit. Seeds exclusively vertical.

A. prostrata group. In the British Isles this group is represented by: *A. prostrata*, *A. glabriuscula*, *A. longipes*, and *A. praecox*. The species are morphologically similar and interfertile in varying degrees and, except for *A. prostrata*, all are restricted to littoral or estuarine habitats. Many coastal populations are made up of hybrid derivatives variously intermediate between two or more species. 2n=18.

1. *A. PROSTRATA* Boucher ex DC., in Lamarck & De Candolle, *Fl. Francaise*, 3rd ed., p. 387 (1805). Lectotype: "Env. du Havre", h. DC. 386, marked "*A. prostrata* Boucher" in herb. DC. (**G**), fide M. Gustafsson in *Opera Botanica*, **39**:21 (1976).

A. prostrata Boucher, *Extrait de la Flore d'Abbeville et du départment de la Somme*, p. 76 (1803). Nomen nudum.

A. triangularis Willdenow, *Sp. Pl.*, **4**:963 (1806). (Lectotype: sheet number 3, "Ipse legi 1804 in Lido di Venezia" initialled "W" and marked "Atr. triangularis", in herb. Willdenow (**B**), fide Taschereau in *Can. J. Bot.*, **50**:1583 (1972)).

A. oppositifolia DC., *Rapports sur les voyages botaniques et agronomiques*, p. 12 (1813). (Lectotype: specimen h. DC. 390 marked "*Atriplex oppositifolia*" in herb. DC. (**G**), fide M. Gustafsson in *Opera Botanica*, **39**:23 (1976)).

A. latifolia Wahlenberg in *Svensk Botanik*, **9**:628 (1824). (Lectotype: Drawing No. 628, in *Svensk Botanik*, **9**:628 (1824), fide M. Gustafsson in *Opera Botanica*, **39**:23 (1976)).

A. deltoidea Babington, *Primitiae Florae Sarnicae*, p. 82 (1839). (Lectotype: Guernsey, Fort George, 1837, *C.C. Babington* (**CGE**), fide M. Gustafsson in *Opera Botanica*, **39**:23 (1976)).

A. hastata sensu Aellen in *Fl. Europaea*, **1**:97 (1964), and sensu auct. angl. non L. The species that Linnaeus called *A. hastata* is the plant presently called *A. calotheca* (Raf.) Fries. (Lectotype: sheet 1221.17 marked "hastata" (**LINN**), fide Taschereau in *Can. J. Bot.*, **50**:1585 (1972)).

Plants 10–100 cm, erect, ascending, decumbent or procumbent. Stems striate, subangular to angular, green and stramineous striped or ± reddish. Branches opposite or sub-opposite up to about two-thirds from the base. Foliage green or reddish, non-succulent; mature leaves finely farinose or glabrous; juvenile and upper leaves glabrous to finely farinose above, grey-farinose to densely white-lepidote below. Lower leaves 2–11 cm long, 2–10 cm wide, triangular with a pair of obtuse out-pointing basal lobes; margins entire, dentate or irregularly toothed; apex acute to obtuse; base truncate to subcordate or broadly obtuse. Upper leaves smaller, triangular or lanceolate, with or without basal lobes; margins entire or toothed. Inflorescence 2–9 cm long, spiciform, composed of contiguous or irregularly spaced glomerules, terminal on stems and branches and on short stems from the axils of upper leaves, leafless except at the base. Bracteoles 2–6 mm long, sessile, triangular to triangular-ovate; apex broadly acute; base truncate to obtuse; margins entire or dentate, united at the base, lateral angles rounded and not strongly developed; herbaceous and thin or ± thickened by the presence of spongy tissue; dorsal surface smooth or tuberculate, venation obscure or prominent. Two seed types present and distinct. Brown seeds 1.5–3.0 mm wide, orbicular; radicle sub-basal, obliquely up-pointing to out-pointing. Black seeds 1.0–2.5 mm; radicle basal, out-pointing. 2n=18. Fig. 3.

HABITAT AND DISTRIBUTION

Halophyte, ruderal and anthropophile, common in silt, sand and shingle on sea beaches and in salt marshes around the coast except in northern Scotland (Fig. 4, omitting unconfirmed, earlier northern records). It is a characteristic component of all inland salt marsh vegetation. The ruderal and anthropophilic biotypes, morphologically indistinguishable from the halophytic variants, are transient colonizers of freshly disturbed soil. They occur with *A. patula* along roadsides and edges of walkways and in waste ground by rubbish tips and on demolished building sites. In northern Scotland, Orkney and Shetland, *A. prostrata* has frequently been confused with hybrid derivatives between other members of the *A. prostrata* group. The species reaches its northern limits in Scotland in approximately the same latitudes as *A. littoralis*. On the east coast, the most northerly record is 3 km north-east of Dingwall, E. Ross, v.c. 106. On the west coast, the most northerly record is from Dumbuck, Dunbarton, v.c. 99. Two collections from disturbed ground on Fair Isle, Shetland, v.c. 112, are introductions of the ruderal biotype of the species and do not represent extensions of its natural range. The absence of *A. prostrata* further northward is coupled with the frequent presence of two hybrids: *A. longipes* × *A. prostrata* and *A. longipes* × *A. glabriuscula*.

FIGURE 3. *Atriplex prostrata.*

REPRODUCTIVE BIOLOGY

Facultatively autogamous and primarily wind pollinated but also visited by syrphid flies that feed on the pollen. Flowering August to September; seed set September to November. The staminate and pistillate flowers, closely clustered together in tight glomerules, mature and open almost simultaneously. This greatly lessens the opportunity for cross pollination. The seed, especially of the ruderal biotypes, consists mostly of the small black type. Unlike the small black seeds of *A. patula* these seeds show no differences in germination response. In *A. prostrata*, the small black seeds germinate at the same rate and to the same extent as the large brown seeds.

2. *A. GLABRIUSCULA* Edmondston, *Fl. Shetland*, p. 39 (1845).

Neotype: Keiss, near Wick, Caithness, 19.IX.1930, *M. L. Wedgewood* (**K**), fide M. Gustafsson in *Opera Botanica*, **39**:15 (1976). Excellent topotype material is: sheet 739, Baltasound, Unst, Shetland, 27.VIII.1887, *W. H. Beeby* (**SLBI**).

A. babingtonii Woods, *Tourist's Fl.*, p. 316 (1850). (Neotype: England, Isle of Wight, shore between Springfield and Nettlestone near Ryde, 26.VIII.1842, the left hand specimen (**K**). The description is probably based on a form of *A. rosea* sensu Babington *Trans. Proc. bot. Soc. Edinb.*, **1**: 13 (1841), fide M. Gustafsson in *Opera Botanica*, **39**: 15 (1976)).

A. glabriuscula var. *pseudocalotheca* Bennett, *Trans. Proc. bot. Soc. Edinb.*, **20**: 1 (1928). (Topotype material in herb. Arthur Bennett (**BM**)).

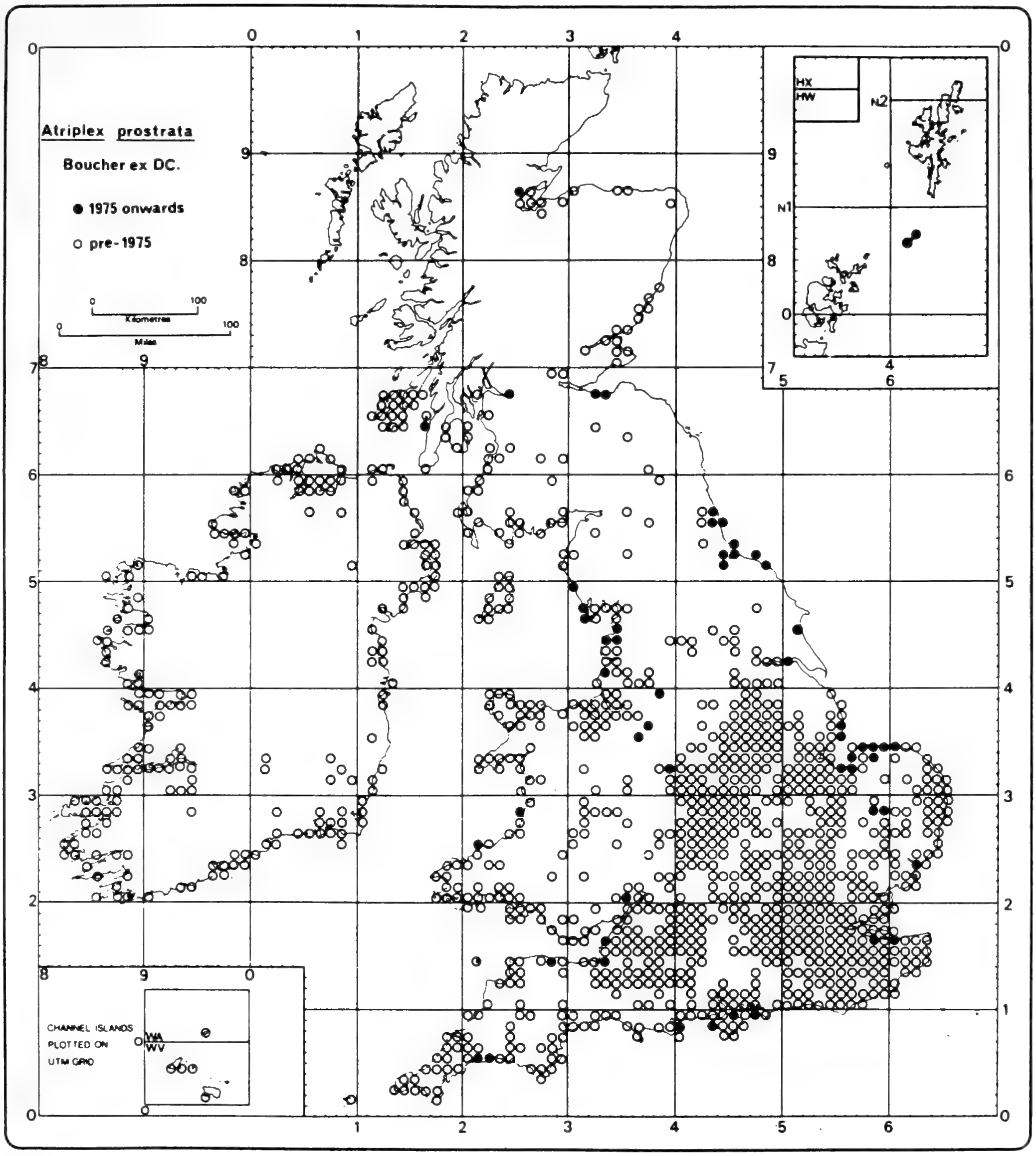


FIGURE 4. Distribution of *Atriplex prostrata* in the British Isles.

Plants 20–90 cm, prostrate, decumbent or less commonly erect. Stems striate, angular, green and stramineous striped, stout, tough-herbaceous. Branches opposite only at the base, swollen at attachment to the main stem. Foliage green, frequently succulent; mature lower and upper leaves glabrous or sparsely fine-farinose about the base of the main veins above and sparsely farinose below; the most juvenile leaves densely farinose above and below. Lower leaves 2–7 cm long, 2–6 cm wide, triangular with a pair of out-pointing to upcurving basal lobes; margins sinuate-dentate, irregularly toothed or rarely almost entire; apex acute to obtuse; base obtuse to truncate or rarely subcordate. Upper leaves smaller, outline highly variable, lanceolate or triangular, with or without basal lobes; margins entire or toothed. Inflorescence 2–15 cm long, spiciform, composed of loose, irregularly-spaced glomerules, terminal on upper stems and branches and from the axils of upper leaves, frequently with much reduced leaves subtending the glomerules up to about two-thirds from

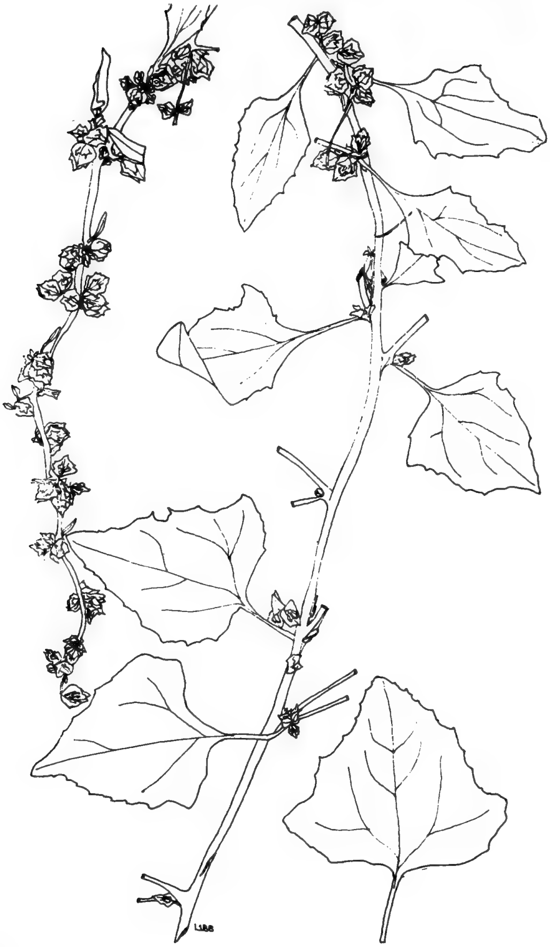


FIGURE 5. *Atriplex glabriuscula*.

the base. Bracteoles 4–10 mm long, sessile, rhombic; apex broadly acute; base broadly cuneate to obtuse or rounded; margins entire or dentate, united up to the middle; lateral angles rounded and not strongly developed; much thickened especially at the base by the presence of spongy tissue; dorsal surface tuberculate, muricate or smooth, venation obscure. Seeds 2.0–4.0 mm wide, mostly dark brown to black (rarely two types present), dull, smooth, ovate to orbicular, flattened or irregularly biconvex; radicle median and usually strongly up-pointing. $2n=18$. Fig. 5.

HABITAT AND DISTRIBUTION

Obligate halophyte confined to the littoral zone of more or less exposed sand or shingle coastal beaches. Records of this species occurring inland (Chapman 1960; Perring & Walters 1962; Lee 1975) are erroneous. Because of the frequency with which this species has been confused with hybrid derivatives between other members of the *A. prostrata* group, all distribution records for it in the British Isles need to be re-examined. A partial distribution, based on my field work and the B.S.B.I. survey, is given in Fig. 6, but the species is much more common than the number of distribution dots would suggest. *Atriplex glabriuscula* is absent from the coasts of Yorkshire, Lincolnshire and Norfolk (v.cc. 61, 54, 53, 28, 27). The Yorkshire coast needs further investigation. The Lincolnshire coast is affected by severe habitat disturbance: intensive human recreational use, military use, extensive land reclamation, sea defence wall-building, cattle grazing and intensive rabbit grazing.

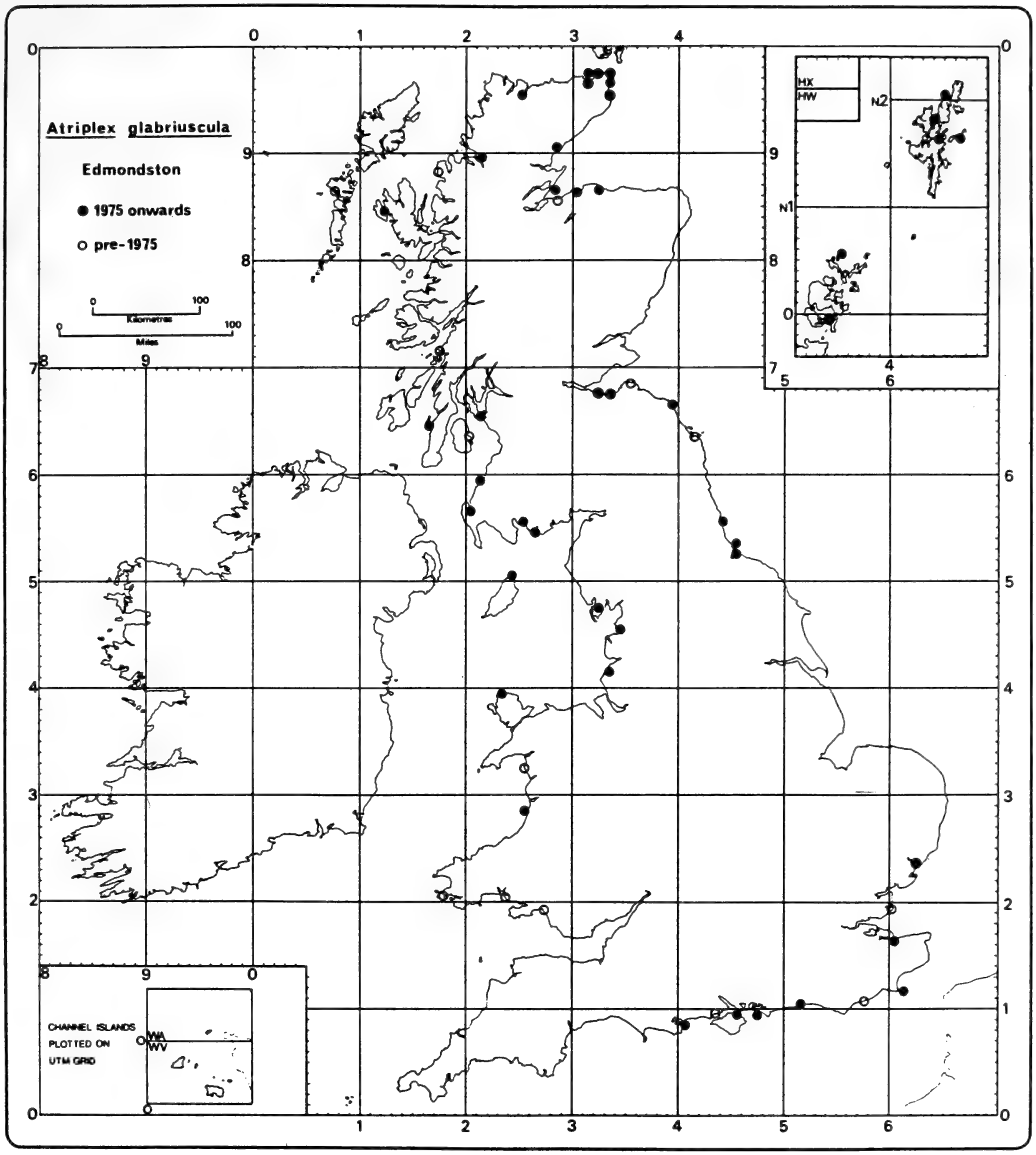


FIGURE 6. Distribution of *Atriplex glabriuscula* in the British Isles.

The northern Norfolk coast is also affected by reclamation, sea-wall defence and drainage, but other ecological factors may be influencing the distribution of *A. glabriuscula* here. Adam (1978) confirmed the distinctiveness of the northern Norfolk salt marshes. He noted that they show vegetational and floristic links with Mediterranean salt marshes. The ecological niche occupied by *A. glabriuscula* in other regions is here occupied by hybrid derivatives between *A. longipes* and *A. prostrata*.

REPRODUCTIVE BIOLOGY

Facultatively autogamous and primarily wind pollinated. Insects observed feeding on *A. glabriuscula* and crawling over the flowers probably play only a very minor role as pollinators in the windy habitat where this species grows. Flowering July to August; seed set September to October. The staminate and pistillate flowers, closely clustered together at anthesis, mature and open almost simultaneously. This lessens the opportunity for cross pollination. *A. glabriuscula* is well adapted to dispersal by sea. The thick firm bracteoles, united up to about the middle, retain the seed while it is in the water. The large air-filled cells of spongy tissue at the base of the bracteoles give them high buoyancy. Under laboratory conditions 71% of the bracteoles examined were still floating after 24 days in continuously agitated sea water (Gustafsson 1973a). The seeds exhibit a marked dormancy. Those planted in the greenhouse will not germinate unless exposed for some time to the fluctuating weather conditions outdoors (Taschereau 1972, 1979). In the laboratory, the seeds can be induced to germinate within nine days by exposing them to alternating daily temperatures of 10°C and 30°C (Ignaciuk & Lee 1980). Seed germination on the north-western coast of England begins during the last week of April, four weeks after the equinoctial spring tides. The main germination occurs in May with a small amount in June. Ignaciuk & Lee (1980), who observed germination on the English coast, pointed out that the alternating temperature requirement of *A. glabriuscula* seeds delays germination until after the equinoctial tides, the period of greatest environmental instability. The amplitude of the diurnal temperature cycle, noted these authors, decreases rapidly with increasing sand depth. (In measurements by Ignaciuk it was halved with each 9 cm increase in depth). Thus, the

FIGURE 7. *Atriplex longipes.*

alternating temperature requirement also prevents the seed with its limited perisperm from germinating beyond depths greater than it can overcome.

3. *A. LONGIPES* Drejer, *Fl. Excurs. Hafniensis*, p. 107 (1838).
Lectotype: Denmark, Copenhagen, Flaskekroen, sheet L92/74 no. 1, *Drejer* (**C**), fide Jones in *Watsonia*, **10**: 250 (1975).
A. prostrata Boucher ex DC. var. *longipes* (Drejer) Meijden in *Gorteria*, **11**: 119 (1982).

Plants 20–90 cm, erect or spreading, stems striate, subangular, green and stramineous striped. Branches opposite only at the base or rarely higher in large specimens. Foliage green at maturity becoming yellow with senescence, succulent; mature and juvenile leaves glabrous. Lower leaves 4–6

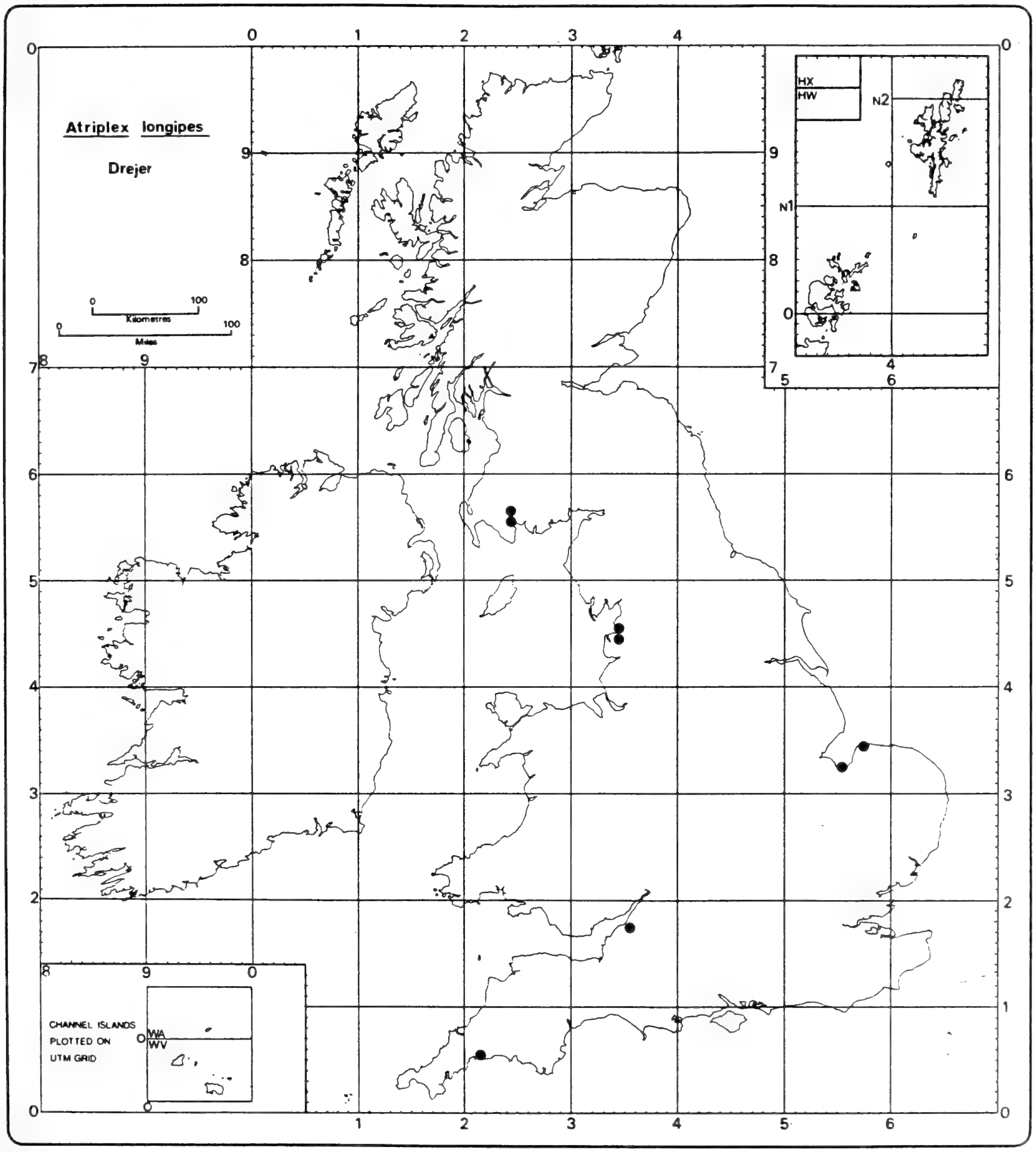


FIGURE 8. Distribution of *Atriplex longipes* in the British Isles.

cm long, 3–5 cm wide, narrowly triangular with a pair of out-pointing or forward-curving basal lobes; margins entire or irregularly toothed; apex acute; base cuneate. Upper leaves lanceolate to linear, without basal lobes or with one small lobe or a pair of weakly developed lobes; margins entire. Inflorescence 10–15 cm long, spiciform, composed of loose irregularly-spaced glomerules, terminal and in the axils of upper leaves and branches, frequently with much reduced leaves subtending the glomerules up to about two-thirds from the inflorescence base. Bracteoles consisting of two forms on the same plant: a smaller, shortly stalked to sessile, thin-herbaceous but non-foliaceous form occurring mostly in the terminal parts of the inflorescence; a larger, long-stalked, thin-herbaceous and frequently foliaceous form occurring in the mid to lower region of the inflorescence and particularly in the axils of the upper leaves and branches. Smaller bracteoles 5–10 mm long on stalks 0.5–1.0 mm long or sessile, rhombic or elongate-triangular; apex acute; base broadly obtuse or cuneate; margins mostly entire, united only at the base; lateral angles pointed, not strongly developed, dorsal surface mostly smooth, venation obscure or prominent. Larger bracteoles 10–25 mm long on stalks 5–25 (–30) mm long, ovate-lanceolate; apex acute; base cuneate to broadly obtuse; margins entire or with a few teeth, united only at the base; lateral angles pointed and strongly developed; dorsal surface smooth or slightly muricate; venation pronounced, forming a reticulate pattern towards the base. Two seed types present. Brown seeds 2.0–3.0 (–3.5) mm wide, orbicular; radicle basal to sub-basal, out-pointing. Black seeds 1.5–2.0 mm wide, orbicular; radicle basal, out-pointing. 2n=18. Fig. 7.

FIGURE 9. *Atriplex praecox.*

HABITAT AND DISTRIBUTION

Obligate halophyte confined to tall salt marsh vegetation bordering estuaries. *A. longipes* grows on a silty substratum in relatively undisturbed sites flooded with brackish water during the highest tides. It is associated with *Aster tripolium* in stands dominated by *Juncus maritimus* and at the margins of *Phragmites australis* stands. In Britain, it is widely distributed, occurring in Kirkcudbrightshire, Norfolk and Cornwall, but always it is local, usually rare and commonly associated with *A. prostrata* hybrids that make it difficult to detect. Distribution in the British Isles is given in Fig. 8.

REPRODUCTIVE BIOLOGY

Facultatively autogamous and primarily wind pollinated. Flowering (?) July to August. Fruiting mid-August to early September. The flowering times can only be inferred because only fruiting

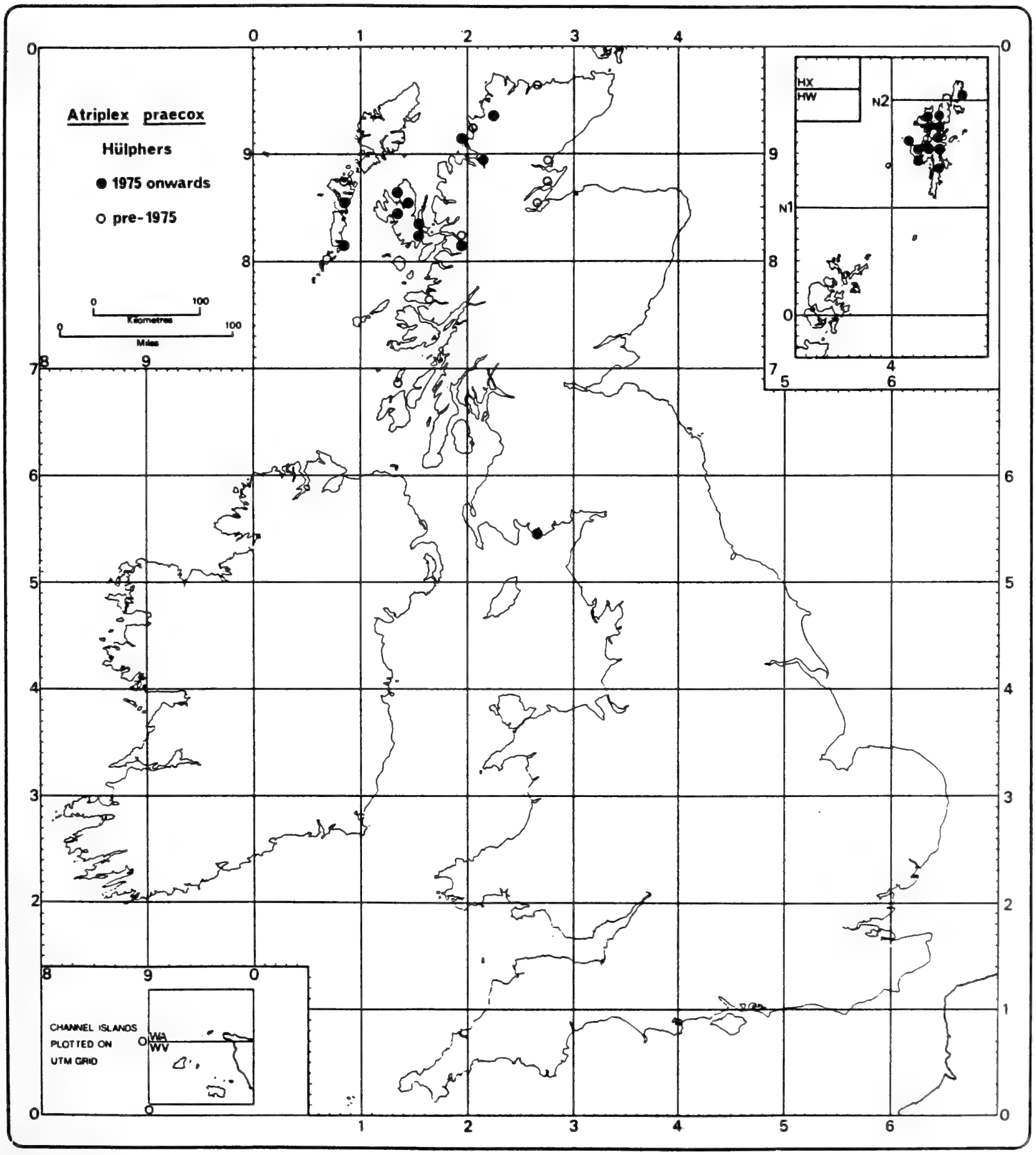


FIGURE 10. Distribution of *Atriplex praecox* in the British Isles.

material has been observed in the British Isles. Staminate and pistillate flowers occur together in the terminal inflorescence, but exclusively pistillate flowers occur singly or a few together in the upper stem and leaf axils. *A. longipes* in Britain, as in Scandinavia (Gustafsson 1972), exhibits distinct protogyny. The pistillate flowers in the leaf axils extend a pair of receptive stigmas several days before the staminate flowers open and shed their pollen. Thus, the opportunity for cross-pollination is increased.

4. *A. PRAECOX* Hülphers, in Lindman, *Svensk Fanerogamflora*, p. 228 (1918).
Lectotype: Sweden, Uppland, Ljusterö s:n, Särsö 18.VII.1912, *A. Hülphers* (marked *A. praecox*) (**S**), fide M. Gustafsson in *Opera Botanica*, **39**: 19 (1976).
A. nudicaulis Boguslaw, *Lesn. Zur.*, **1**: 30 (1846). (Type Locality: U.S.S.R., in the vicinity of Archangel). Type material inquired for unsuccessfully at **LE** by M. Gustafsson whom I have followed in listing this name as a synonym.
A. longipes Drejer subsp. *praecox* (Hülphers) Turesson in *Lunds Univ. Årsskr.*, N.F. Adv. 2, **21**(4): 6 (1925).

Plants 3–10 (–15) cm, erect or procumbent. Stems terete or sub-angular, green or red. Branches opposite up to about two-thirds from the base, the lowermost ones often long-spreading and sometimes longer than the central axis. Foliage bluish-green, often reddish tinged, succulent; mature leaves glabrous, juvenile and upper leaves finely farinose. Lower leaves 1.0–3.0 cm long, 0.5–1.3 cm wide, ovate or lanceolate with a pair of short, out-pointing basal lobes; margins entire or with a few short teeth; apex acute or obtuse; base cuneate to attenuate. Upper leaves smaller, lanceolate to linear, without basal lobes; margins entire. Inflorescence entirely axillary or also terminal, 1–3 cm long, composed of loose irregularly spaced glomerules, leafy throughout. Bracteoles 3–5 mm long, sessile or with stalks 0.5–1.5 mm long, rhombic-ovate or triangular-ovate; apex acute or acuminate; base cuneate, obtuse to truncate; margins entire, united at the base; lateral angles rounded, not developed or slightly unilaterally developed; thin-herbaceous or membranous; dorsal surface smooth, venation obscure. Seeds 1.5–3.0 mm wide, ovoid or sub-orbicular, 0.1–0.4 mm longer than wide, not distinctly dimorphic, black or dark brown, biconvex, lustrous, smooth or patterned; radicle sub-basal, obliquely up-pointing to out-pointing. 2n=18. Fig. 9.

HABITAT AND DISTRIBUTION

Obligate halophyte restricted to the margins of semi-protected sea inlets in northern coastal habitats. It occurs in shingle or sand in the low beach zone below the *Cakile-Atriplex* association, barely above the high water fucoid zone, in a region devoid of other terrestrial species. The most commonly reported habitat is close to the salt water in shingle bordering sea lochs. Here, *A. praecox* plants frequently form a distinctive red zone of very low, sparse vegetation clearly discontinuous from the strand plants of the middle beach. Distribution in the British Isles is shown in Fig. 10.

REPRODUCTIVE BIOLOGY

Facultatively autogamous and primarily wind pollinated. Flowering June to July; seed set August to September. The species is protogynous, the pistillate flowers extending receptive stigmas several days before the staminate flowers open and shed their pollen. *A. praecox* matures earlier than most other *Atriplex* species in Britain and disappears from its habitat before October. Reproductive isolation is probably facilitated to some extent by its earlier flowering time and by the specialized ecological niche which it occupies.

5. *A. LITTORALIS* L., *Sp. Pl.*, p. 1054 (1753).
Lectotype: L. 3613, No. 1 in herb. Royen (**L**), fide Taschereau *Can. J. Bot.*, **50**: 1581 (1972).
A. serrata Hudson, *Fl. Angl.*, p. 377 (1762). (Lectotype: drawing of *Atriplex angustifolia dentata* in the upper right hand corner of the page, t.7f.4. of J. Petiver's *Herbarij Britannici* (1712–15), cited by Hudson).
A. marina L., *Mant. Pl.*, p. 300 (1771).
A. littoralis var. *serrata* S. F. Gray, *Nat. Arr.*, p. 282 (1821).
A. patula var. *littoralis* A. Gray, *Man.*, 5th ed., p. 409 (1867) pro parte.

FIGURE 11. *Atriplex littoralis.*

Plants 30–150 cm, erect. Stems stout, striate, sub-angular, green and stramineous striped, frequently reddish. Branches opposite only at the base. Foliage green at maturity becoming yellowish or reddish with senescence, not or slightly succulent; mature lower and upper leaves glabrous; juvenile leaves slightly scurfy. Lower leaves 2–10 cm long, 0.5–1.5 cm wide, linear to linear-oblong, without basal lobes or with a varying number of leaves possessing one lobe or a pair of out-pointing to obliquely forward-pointing basal lobes; margins entire or irregularly repand-dentate; apex acute to acuminate; base attenuate. Upper leaves reduced, linear, without basal lobes; margins usually entire. Inflorescence long (up to 20 cm), interrupted spiciform, of densely packed glomerules widely spaced toward the base but becoming contiguous toward the apex, terminal and from the axils of upper leaves, leafless except at the base. Bracteoles 3–6 mm long, sessile, triangular-ovate; apex acute or lingulate, frequently recurved at maturity; base cuneate to obtuse, or truncate; margins denticulate, united at the base; lateral angles rounded, not or weakly developed; usually thick-spongy; dorsal surface muricate and commonly bi-tuberculate, venation obscure. Two seed types present but the black type usually more abundant. Brown seeds 2.0–2.5 mm wide, orbicular or transversely elliptic, radicle sub-basal, obliquely up-pointing to out-pointing. Black seeds 1.3–2.0 mm wide, orbicular or transversely elliptic, radicle sub-basal, out-pointing to obliquely up-pointing. 2n=18. Fig. 11.

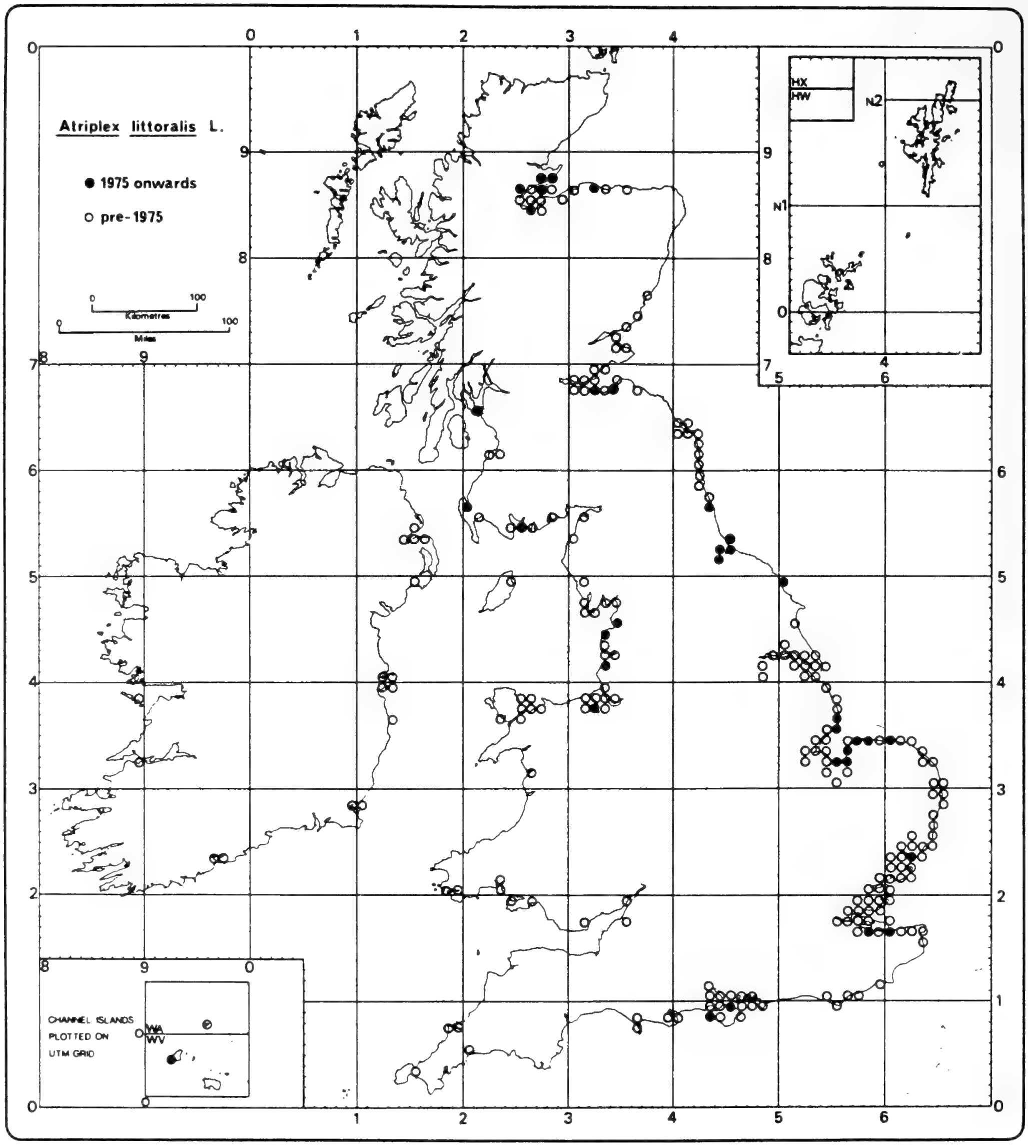


FIGURE 12. Distribution of *Atriplex littoralis* in the British Isles.

HABITAT AND DISTRIBUTION

Obligate halophyte confined to coastal habitats. *A. littoralis* is frequent in silt at the mouths of estuaries, in sand on more or less sheltered beaches and as a constituent of coastal salt marsh vegetation. With *A. prostrata*, it is frequently an early colonizer of earthen sea walls. Occasionally, *A. littoralis* is reported as a casual along roadsides inland, but such plants rarely persist more than one or two years. Distribution in the British Isles is given in Fig. 12. Here, *A. littoralis* reaches its northern limits in northern Scotland. On the east coast, the most northerly record is Balintore, E. Ross, v.c. 106. It is absent from Loch Fleet, about 15 miles further north in East Sutherland, v.c. 107. On the west coast, the most northerly record is Kilchattan Bay, Isle of Bute, v.c. 100. No specimens were seen from the Orkney Islands nor was the county recorder for that region able to find any. The distribution records from there in Perring & Walters (1962) may be a mistake.

REPRODUCTIVE BIOLOGY

Facultatively autogamous and primarily wind pollinated but also frequently visited by syrphid flies. Flowering July to August; seed set September to October. Staminate and pistillate flowers occur together in the terminal inflorescence but the flowers in the upper leaf axils are primarily and sometimes exclusively pistillate. Protogynous, the pistillate flowers extending a pair of receptive stigmas several days before the staminate flowers open and shed their pollen. The bracteoles in some strains remain attached to the inflorescence axis rather than falling with the seed. At maturity the tips of these bracteoles become recurved exposing the seed which is shaken out by the action of the wind on the rigid woody stalk. In other strains the bracteoles and seed fall together. In cultivation, *A. littoralis* seeds are the first *Atriplex* seeds to germinate but there is no information on the germination dates of plants in their natural habitat. The small black seeds are generally more abundant, comprising 70–80% of the seeds of most plants in Britain. The proportion ranges from 50–86% however, and some of the seeds categorized as brown are very dark brown and somewhat biconvex. In the laboratory, both black and brown seeds germinate readily at about the same rate within two weeks. There is no dormant period. A sweet, sticky exudate is produced in droplets on the stems and main branches of *A. littoralis* before and at flowering, but how this may be related to the reproductive biology is not known.

FIGURE 13. *Atriplex patula*.

6. *A. PATULA* L., *Sp. Pl.*, p. 1053 (1753).
Lectotype: No. 1221.19 in Herb. Linné (**LINN**), fide Taschereau in *Can. J. Bot.*, **50**: 1574 (1972).
A. erecta sensu Smith, *Fl. Brit.*, p. 1093 (1804).
A. angustifolia sensu Smith, *Fl. Brit.*, p. 1093 (1804).
A. patula var. *bracteata* sensu Moss and Wilmott, in *Camb. Br. Fl.*, p. 174 (1914). The taxon that Westerlund in *Sveriges Atripl.*, p. 57 (1861) called *A. patula* var. *bracteata* is a hybrid derivative between *A. longipes* and *A. prostrata*. (Lectotype: sheet marked "*Atriplex patula* Lin. –*bracteata* Westerl.," and initialed, "C.A.W." (**S**)).

Plants 15–100 cm, erect, ascending or prostrate. Stems angular, green and stramineous striped. Branches opposite to sub-opposite up to about two-thirds from the base. Foliage bright green at

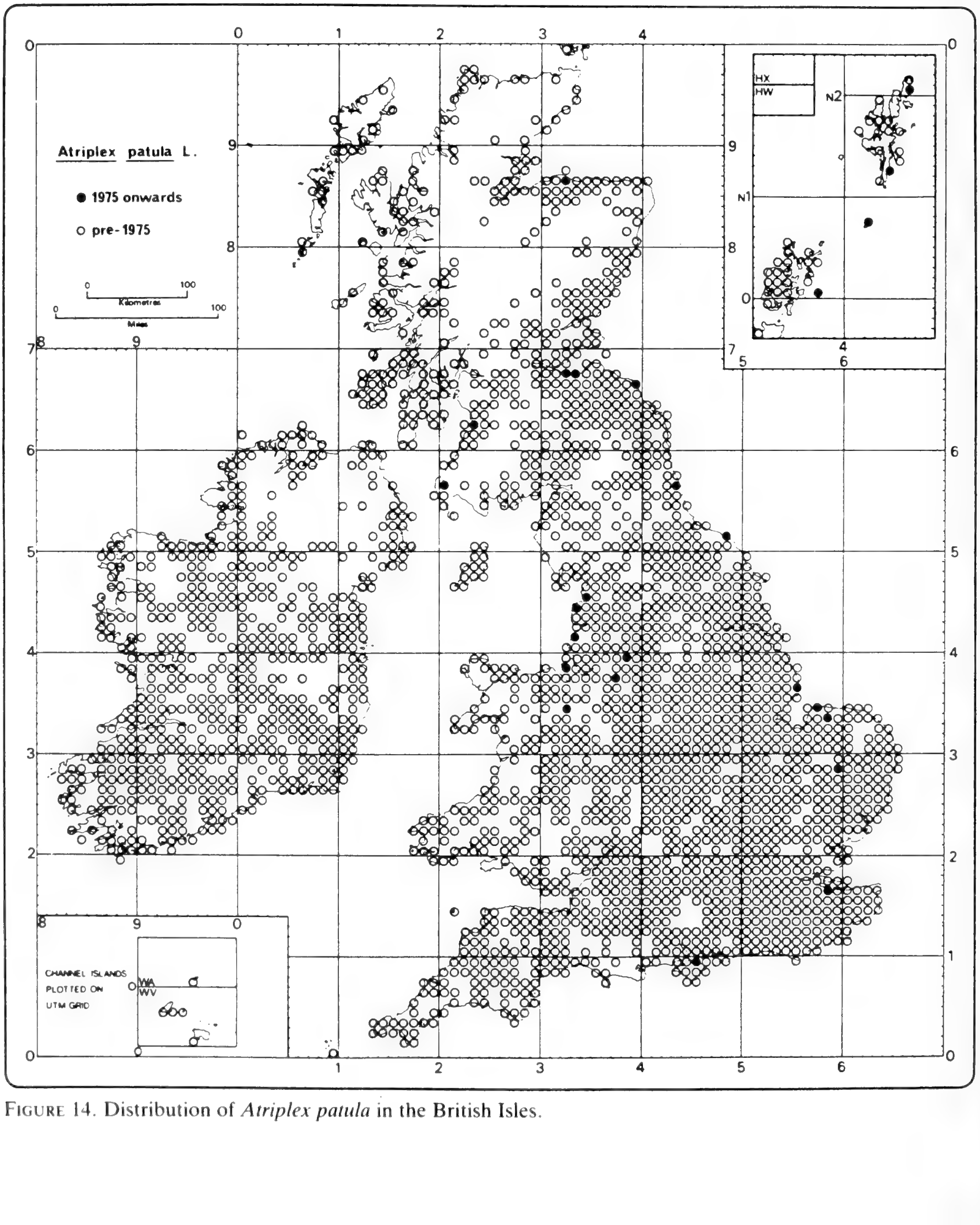


FIGURE 14. Distribution of *Atriplex patula* in the British Isles.

maturity, not changing with senescence, non-succulent; mature lower and upper leaves glabrous; juvenile leaves with fine, sparsely distributed farina (visible at ×12) on both sides but denser on the undersurface. Lower leaves 4–9 cm long, 1.5–4.5 cm wide, ovate-lanceolate with a pair of falcate, forward-pointing basal lobes or without lobes; margins irregularly serrate or entire; apex acute; base cuneate. Upper leaves smaller, narrowly lanceolate to oblong-linear without or with basal lobes; margins entire or irregularly serrate. Inflorescence 1–6 cm long, interrupted-spiciform, composed of densely packed glomerules becoming contiguous towards the apex, terminal and axillary, leafless or with reduced leaves in the lower portions. Bracteoles 3–7 (–20) mm long, sessile or with stalks 0.5–4.0 mm long, rhombic or triangular-rhombic; apex acute or acuminate; base cuneate to broadly obtuse; margins entire or with a few short teeth, united up to the middle; lateral angles pointed, often strongly developed; herbaceous and thin, sometimes becoming foliaceous, spongy tissue never present; dorsal surface smooth or with few irregular short laciniate appendages, venation obscure or prominent towards the base. Two seed types present but intermediate types are frequent and some strains produce mostly small black seeds. Brown seeds 2.0–3.5 mm wide, orbicular, radicle sub-basal, obliquely up-pointing. Black seeds 1.5–2.5 mm, orbicular; radicle sub-basal, out-pointing. 2n=36. Fig. 13.

HABITAT AND DISTRIBUTION

Ruderal, fimicolous and anthropophilous weed of roadsides, pathways and barnyards, and a transient colonizer of freshly disturbed soil. This species frequently occurs in cities with *A. prostrata* on waste ground, at the margins of sidewalks, by rubbish tips and in disturbed soil on demolished building sites. *A. patula* rarely occurs in the littoral zone of coastal beaches. Along the coast it is primarily confined to the weedy ecotone between land and sea. It frequently occurs in soil on eroding coastal banks and about the nests of seagulls on coastal islands. Distribution in the British Isles is given in Fig. 14.

REPRODUCTIVE BIOLOGY

Facultatively autogamous and primarily wind pollinated but also visited by syrphid flies that feed on the pollen. Flowering mid-June to October; seed set September to November. The staminate and pistillate flowers are closely clustered together in tight glomerules. *A. patula* exhibits a slight protogyny, the female flowers extending receptive stigmas about one to four days before the anthers open. This species is the earliest flowering *Atriplex* in the British Isles. In Manchester, some plants begin flowering as early as 1st June. In the laboratory, the brown seeds germinate within about two weeks but few black seeds will germinate without being scarified and subjected to a period of alternating temperatures.

Section *SCLEROCALYMMA* Ascherson, *Fl. Brandenb.*, p. 578 (1864).

Stems whitish, pale brown or reddish. Venation kranztypus. Flowers monoecious, the pistillate ones all bracteolate and lacking a perianth. Bracteoles united up to the middle becoming cartilaginous in fruit. Seeds exclusively vertical.

7. *A. LACINIATA* L. *Sp. Pl.*, p. 1053 (1753).
Lectotype: in Hortus Siccus Cliffortianus (**BM**), fide Taschereau in *Can. J. Bot.*, **50**: 1591 (1972).
A. arenaria Woods in *Phytologist*, **3**: 593 (1849), non Nuttall.
A. maritima Hallier in *Bot. Z. Beitr.*, p. 10 (1863), non Crantz nec Pallas.
A. sabulosa Rouy in *Bull. Soc. bot. Fr.*, **37**: 20 (1890).

Plants 6–30 cm, decumbent with wide-spreading, ascending lower branches. Stems smooth or sub-angular, reddish or yellowish, more or less sparsely scaly, straight; much branched in a diffuse asymmetrical pattern. Lowermost one to three pairs of branches opposite or sub-opposite, the remainder alternate. Foliage whitish-green or greyish-green, non-succulent; mature and juvenile leaves covered with a fine scaly layer on both surfaces but more densely covered below. Lower leaves 1.5–4.0 cm long, ovate to lance-ovate, sinuate-dentate with larger basal lobes; base cuneate to a short petiole; apex obtuse. Upper leaves smaller, narrower, lanceolate or oblong, sinuate-dentate or entire, obtuse, mucronate. Inflorescence glomerulate in upper leaf axils. Bracteoles 6–7 mm long,

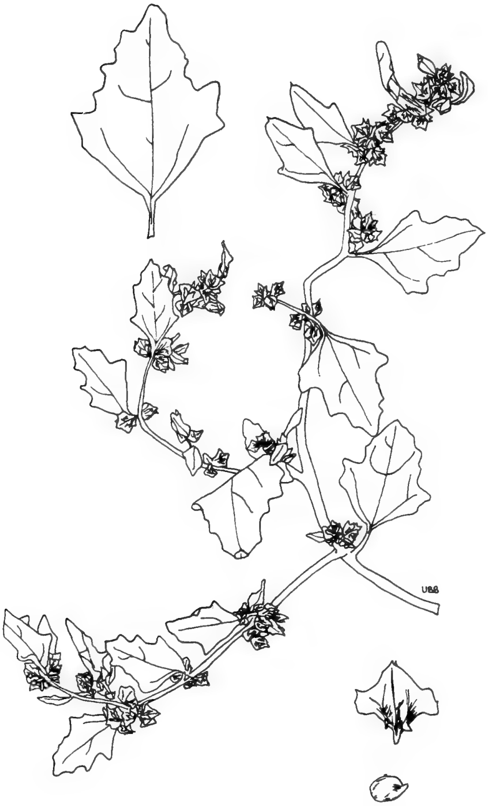


FIGURE 15. *Atriplex laciniata.*

sessile or with short stalks, broadly rhombic, whitish-green becoming scaly-black with maturity; apex acute; base cuneate; margins entire or with a few short teeth, united up to the middle, with lateral angles obtuse and strongly produced; cartilaginous, becoming thickened and hardened in the lower half, spongy tissue never present; dorsal surface smooth or with irregular pointed or flattened and wing-like tubercles or projections in the lower half, venation ± prominent. One seed type present: light brown, 3.5–4.0 mm wide, transverse-elliptic, dull, smooth; radicle median out-pointing to ascending, thick and prominent with apex strongly produced. $2n=18$. Fig. 15.

HABITAT AND DISTRIBUTION

Coastal halophyte of sand or sand and cobble beaches. Widespread in the British Isles but often local. Where it occurs, it is usually present in low numbers as more or less widely-scattered individuals and after some years absence it may reoccur in a former locality. Observed in abundance only at Dunnet Bay, Caithness, Scotland. Distribution in the British Isles is given in Fig. 16.

REPRODUCTIVE BIOLOGY

Facultatively autogamous and primarily wind pollinated. Isolated plants grown in the greenhouse produced normal amounts of viable seed (Taschereau unpublished). Flowering August to September; seed set September to October. *A. laciniata* is well adapted to dispersal by sea. The cartilaginous bracteoles, united up to the middle, tenaciously retain the seed and soften little after soaking in sea water for several days. In the laboratory, bracteoles of this species floated in sea water for up to ten days (Taschereau 1970). Ignaciuk & Lee (1980) immersed bracteoles in constantly agitated salt water (600 mM NaCl). After five days, 20% of the bracteoles remained floating, but by eight days all had sunk. Ignaciuk & Lee (1980) found that seeds immersed in salt water (600 mM

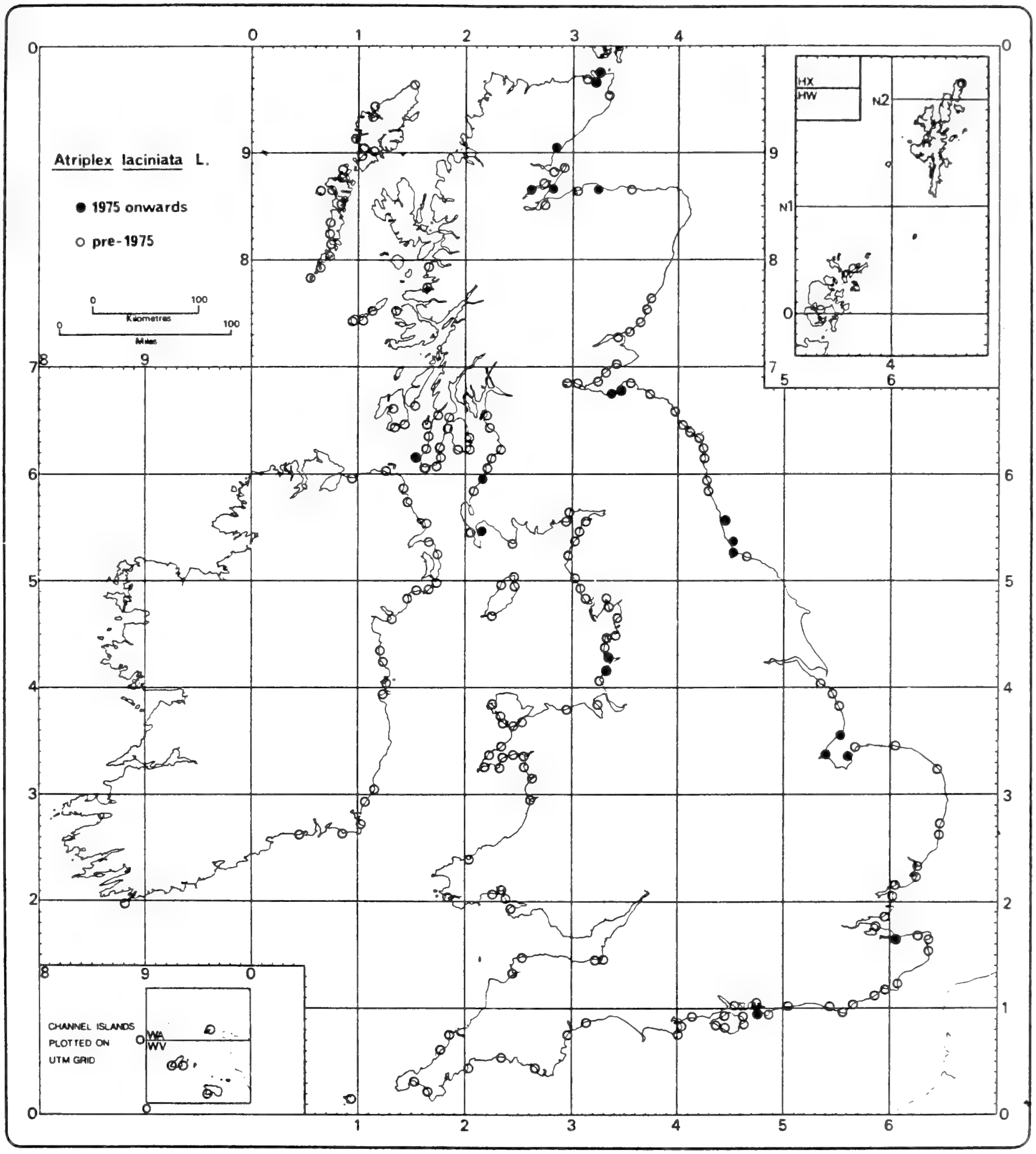


FIGURE 16. Distribution of *Atriplex laciniata* in the British Isles.

NaCl) for up to 30 days remained viable. Furthermore, these authors report that the seeds could germinate at this salt concentration and produce healthy seedlings although the growth rate of the plants was reduced. The seeds exhibit a marked dormancy. Those planted in the greenhouse will not germinate unless exposed for some time to fluctuating weather conditions outdoors (Taschereau 1970). In the laboratory, however, seeds readily germinate after being exposed to a period of alternating daily temperatures (Ignaciuk & Lee 1980). As in the case of *A. glabriuscula*, noted Ignaciuk & Lee (1980), the alternating temperature requirement of *A. laciniata* delays germination until after the spring equinoctial tides, the period of greatest environmental instability. This mechanism, they observed, also prevents the seed with its limited perisperm reserve from germinating beyond depths greater than it can overcome.

HYBRIDS

A. glabriuscula × *longipes*
Hybrid derivatives between *A. glabriuscula* and *A. longipes* are frequent on exposed coastal beaches in northern England and Scotland. They occur with *A. glabriuscula* in the habitat characteristic of that species in regions where *A. longipes* is absent.

A. glabriuscula × *praecox*
Rare in northern Scotland and Shetland. Occurring in the same habitat as the parent species.

A. glabriuscula × *prostrata*
Rare, from southern England to south-western Scotland and on the eastern coast of England. Occurring in the same habitat as the parent species. Earlier literature reports (Moss & Wilmott 1914; Jones 1975b) of its frequency are unconfirmed.

A. longipes × *prostrata*
Frequent wherever the parent species occur together; occasional inland in salt marshes and waste places. Hybrid derivatives between *A. longipes* and *A. prostrata* are common in sand and shingle on exposed coastal beaches in all regions of the British Isles, frequently in areas remote from one or both parent species.

Gustafsson's (1973b) experimental work with this hybrid in Sweden showed that it is present there as a more or less well-stabilized variant. Comparable plants are frequent in northern Scotland and occasional in Shetland where they occur on exposed coastal beaches, a habitat colonized by neither of the parent species. Occasionally found with *A. praecox* on the shores of somewhat less exposed sea inlets.

A. littoralis × *prostrata*
Occasional on the eastern and western coasts of England in disturbed habitats where both parents are present in abundance.

A. littoralis × *patula*
Known from only one locality in Midlothian, v.c. 83, where both parents were present in disturbed waste ground by the coast.

ACKNOWLEDGMENTS

Mats Gustafsson's work on the *A. prostrata* group in Scandinavia has been fundamental to my understanding of *Atriplex* in the British Isles. I am deeply indebted to him for his personal assistance, many stimulating conversations and for his warm hospitality during my visits to Sweden.

The *Atriplex* Survey undertaken by members of the Botanical Society of the British Isles in co-operation with the Biological Records Centre, Monks Wood, further extended the geographic area covered by this study. To the Centre and to the B.S.B.I. members who took such care in sending me specimens and data, I am grateful. My discussions and field work with Richard P. Libbey, who took me to *Atriplex* sites in Norfolk, were enjoyable and helpful and I benefited also from my visits to and discussions with two former students of the genus, Barbara Hulme and Elizabeth Jones.

The first three years of this study were financed by a scholarship from the National Research Council of Canada. The continuation of the study for a further two years was made possible by the generous financial help I received from John Meredith and the late Hilda Meredith. I acknowledge the help and encouragement of Professor D. H. Valentine, my supervisor during the course of this study. The drawings were prepared by B. U. Borluk.

REFERENCES

Adam, P. (1978). Geographical variation in British saltmarsh vegetation. *J. Ecol.*, **66**: 339–366.

Aellen, P. (1960). *Atriplex*, in Rechinger, K. H., ed. *Hegi Illustrierte Flora von Mitteleuropa*, 2nd ed., **3**: 664–693. München.

Aellen, P. (1964). *Atriplex*, in Tutin, T. G. *et al.*, eds. *Flora Europaea*, **1**: 95–97. Cambridge.

Babington, A. M. (1897). *Memoirs, journal and botanical correspondence of Charles Cardale Babington*, p. 347. Cambridge.

Babington, C. C. (1841). Monograph of the British Atripliceae. *Trans. Proc. bot. Soc. Edinb.*, **1**: 1–17.

Babington, C. C. (1843). *Manual of British Botany*. London.

Bentham, G. & Hooker, J. D. (1896). *Handbook of the British flora*, 6th ed., revised by J. D. Hooker, p. 378. London.

Chapman, V. J. (1960). *Salt marshes and salt deserts of the world*. London.

Cole, M. J. (1961). Interspecific relationships and intraspecific variation of *Chenopodium album* in Britain, I. The taxonomic delimitation of the species. *Watsonia*, **5**: 47–58.

Dreiding, A. (1961). The Betacyanins a class of red pigments in the Centrospermae, in Ollis, W. D., ed. *Recent developments in the chemistry of natural compounds*, pp. 194–221. Oxford.

Druce, G. C. (1928). *British Plant List*, 2nd ed., p. 98. Arbroath.

Gray, A. (1868). *Manual of the botany of the northern United States*. New York.

Gustafsson, M. (1972). Distribution and effects of paracentric inversions in populations of *Atriplex longipes*. *Hereditas*, **71**: 173–194.

Gustafsson, M. (1973a). Evolutionary trends in the *Atriplex triangularis* group of Scandinavia, 1. Hybrid sterility and chromosomal differentiation. *Bot. Notiser*, **126**: 345–392.

Gustafsson, M. (1973b). Evolutionary trends in the *Atriplex triangularis* group of Scandinavia, 2. Spontaneous hybridization in relation to reproductive isolation. *Bot. Notiser*, **126**: 398–416.

Gustafsson, M. (1974). Evolutionary trends in the *Atriplex triangularis* group of Scandinavia, 3. The effects of population size and introgression on chromosomal differentiation. *Bot. Notiser*, **127**: 125–148.

Gustafsson, M. (1976). Evolutionary trends in the *Atriplex prostrata* group of Scandinavia, 4. Taxonomy and morphological variation. *Op. bot. Soc. bot. Lund.*, **39**: 1–63.

Heath, J. & Scott, D. (1974). *Biological Records Centre instructions for recorders*, p. 16. Huntingdon.

Holmgren, P. K., Keuken, W. & Schofield, E. (1981). *Index herbariorum*, 7th ed. Utrecht.

Hulme, B. A. (1957). *Studies on some British species of* Atriplex. Ph.D. thesis, University of Edinburgh.

Hulme, B. A. (1958). Artificial hybrids in the genus *Atriplex*. *Proc. bot. Soc. Br. Isl.*, **3**: 94.

Ignaciuk, R. & Lee, J. A. (1980). The germination of four annual strand-line species. *New Phytol.*, **84**: 581–591.

Jones, E. M. (1975a). Taxonomic studies of the genus *Atriplex* (Chenopodiaceae) in Britain. *Watsonia*, **10**: 233–251.

Jones, E. M. (1975b). *Atriplex*, in Stace, C. A., ed. *Hybridization and the flora of the British Isles*, pp. 185–186. London.

Kent, D. H. & Allen, D. E. (1984). *British and Irish herbaria*. London.

Lee, J. A. (1975). The conservation of British inland salt marshes. *Biol. Conserv.*, **8**: 143–151.

Meijden, R. van der (1970). Biosystematic notes on *Atriplex patula* L., *A. hastata* L. and *A. littoralis* L. (Chenopodiaceae). *Blumea*, **18**: 53–63.

Moss, C. E. & Wilmott, A. J. (1914). *Atriplex*, in Moss, C. E. *The Cambridge British flora*, **2**: 168–182, plates 172–188. Cambridge.

Perring, F. H. & Walters, S. M., eds (1962). *Atlas of the British flora*. London.

Stearn, W. T. (1973). Introduction, in Åsberg, M. & Stearn, W. T. Translation of *Linnaeus's Öland and Gotland Journey 1741*, p. 10. London.

Taschereau, P. M. (1970). *The genus* Atriplex *in Nova Scotia: taxonomy, ecology and distribution*. M.Sc. thesis, Acadia University.

Taschereau, P. M. (1972). Taxonomy and distribution of *Atriplex* species in Nova Scotia. *Can. J. Bot.*, **50**: 1571–1594.

Taschereau, P. M. (1977). *Atriplex praecox* Hülphers: a species new to the British Isles. *Watsonia*, **11**: 195–198.

Taschereau, P. M. (1979). *Taxonomy of the genus* Atriplex *in Great Britain*. Ph.D. thesis, University of Manchester.

Turesson, G. (1919). The cause of plagiotropy in maritime shore plants. *Lunds Univ. Årsskr.*, N.F. Adv. 2., **16**(2): 1–32.

Turesson, G. (1922a). The species and the variety as ecological units. *Hereditas*, **3**: 100–112.

Turesson, G. (1922b). The genotypical response of the plant species to the habitat. *Hereditas*, **3**: 211–350.

Turesson, G. (1925). Studies in the genus *Atriplex*. *Lunds Univ. Årsskr.*, N. F. Adv. 2, **21**(4): 1–15.

Tutin, T. G. (1962). *Atriplex*, in Clapham, A. R., Tutin, T. G. & Warburg, E. F. *Flora of the British Isles*, 2nd ed., pp. 281–283. Cambridge.

(*Accepted March 1984*)

Watsonia, **15**, 211–219 (1985)

Field studies, cultivation experiments and the taxonomy of *Atriplex longipes* Drejer in the British Isles

P. M. TASCHEREAU*

Department of Botany, University of Manchester

ABSTRACT

Atriplex longipes Drejer (Chenopodiaceae), a rare and elusive species known in the British Isles only since 1977, is reported from eight localities. Its rarity in Britain is due to the specialized habitat it occupies and the facility with which it hybridizes with *A. prostrata*. Hybrids with *A. prostrata* are frequent in all localities and cultivation studies reveal that hybrid plants can be morphologically indistinguishable from *A. longipes* s.str. Taxonomic characters separating *A. longipes* from *A. prostrata* are given. The presence of stalked bracteoles is not sufficient to distinguish *A. longipes* from other taxa. Field studies indicate that hybrid derivatives between *A. longipes* and *A. prostrata* and between *A. longipes* and *A. glabriuscula* are occasional to frequent on most coasts of the British Isles. For morphological, genetic, ecological and practical reasons, *A. longipes* is maintained at the species level.

INTRODUCTION

Atriplex longipes Drejer is a member of the *A. prostrata* group (*Hastata* complex). The group comprises a number of partially interfertile and morphologically similar taxa found on the coasts of western Europe and elsewhere. In the British Isles it is represented also by *A. prostrata* Boucher ex DC. (*A. hastata* auct.), *A. glabriuscula* Edmondston and *A. praecox* Hülphers.

Aellen (1964) reported that *Atriplex longipes* was "recently found to be widespread in the British Isles . . .". He noted that it was often confused with *A. prostrata* and *A. glabriuscula* and that "in Britain it has commonly been called *A. patula* var. *bracteosa*". Aellen based his report on data provided by B. Hulme. Jones (1975a) reported on plants she said were "best described as variants in the *A. hastata* complex which resemble *A. longipes*". She concluded that "a few plants very similar to this species have been found in Britain", but that they were "less common in this country than suggested by Hulme". Gustafsson (1976) noted that *A. longipes* had been reported from the British Isles, but stated that all the material he had seen from there could be referred to other species. My search of the major British and Irish herbaria failed to reveal a single specimen of *A. longipes*. The herbarium of B. Hulme contained none and Jones's (1975) specimen from Brean, Somerset (**OXF**!) proved to be a hybrid derivative between *A. longipes* and *A. prostrata*.

In 1977, I reported the occurrence of *A. longipes* at Wigtown Bay, v.c. 73, thus confirming the presence of this species in the British Isles. The British specimens compared well with Scandinavian material in **C**, **LD** and **S** and my determination was confirmed by M. Gustafsson (Taschereau 1977). More specimens were later collected in Norfolk (Libbey 1977) and further field work revealed another locality in south-western England. Despite this, *A. longipes* remains an elusive and exceedingly rare species in Britain, persisting only in relatively undisturbed tall estuarine saltmarsh vegetation.

A. longipes has a mainly Scandinavian distribution and, until 1977, its occurrence outside of this area was unconfirmed. The species has since been reported from Holland and more recently (Garve 1982) from Germany.

Gustafsson's (1972, 1973a, 1973b, 1974, 1976) experimental studies of *A. longipes* and its relationship to other members of the *A. prostrata* group provide the basis for understanding the biology of this species in Britain and elsewhere.

---

*Present address: *Institute for Resource and Environmental Studies, Dalhousie University, Halifax, Nova Scotia, Canada, B3H 3E2*

The present paper reports the results of field and cultivation work with *A. longipes*. It describes the important taxonomic characters of this species and compares them with those of *A. prostrata*. It gives data on the specialized habitat occupied by *A. longipes* in the British Isles and discusses the frequency of hybridization between *A. longipes* and *A. prostrata* here. It gives reasons why *A. longipes* is appropriately maintained at the species level and why this taxon is the key to understanding much of the variation in the coastal members of the *A. prostrata* group in the British Isles.

MATERIALS AND METHODS

FIELD STUDIES

Extensive field studies were made between 1974 and 1978 as part of a broader study of the taxonomy of the genus *Atriplex* in the British Isles (Taschereau 1979). In 1977, this field work was supplemented by a network survey of the coastal *Atriplex* species undertaken through the Botanical Society of the British Isles in co-operation with the Biological Records Centre, Monks Wood Experimental Station. In this way, specimens and data on *Atriplex* species, hybrids, and their habitats were obtained from areas within all the major plant regions of Britain (Heath & Scott 1974) and all coastal regions except the Outer Hebrides and the coasts of Ireland.

CULTIVATION WORK

Seeds were taken from typical herbarium specimens of *A. longipes* collected from three, widely-separated, British populations: Palnure, Kirkcudbrights., v.c. 73; Brancaster, W. Norfolk, v.c. 28; and Penpoll, E. Cornwall, v.c. 2. The seeds were separately sown in the autumn in trays of John Innes Seed Compost and placed in an unheated greenhouse. The seedlings were later transferred to individual pots containing John Innes Potting Compost and repotted as necessary.

A number of seedlings were treated in various ways (Table 1) to investigate the influence of shading, pruning and crowding on bracteole morphology and bracteole stalk development. The plants used in these experiments were grown from seed taken from a single specimen (Brancaster 76–18) that had numerous stalked bracteoles (larger stalks 10–15 mm long).

MEASUREMENTS AND HERBARIUM STUDIES

The following taxonomic characters were examined in both the wild plants and their cultivated offspring: bracteole stalk length, plant height, leaf base angle, lower leaf morphology and the ratio of black:brown seeds produced. (These characters are discussed in detail in Taschereau (1985a)). Evidence of hybridization was provided by progeny tests.

Material from the following herbaria was examined: **ABD**, **BM**, **C**, **CGE**, **DBN**, **E**, **K**, **LD**, **LIV**, **LIVU**, **MANCH**, **NMW**, **OXF**, **S**, **SLBI**, **TCD** (abbreviations are according to Kent & Allen (1984), and Holmgren *et al.* (1981)). My specimens are deposited in **MANCH**.

RESULTS

HABITAT

In the British Isles, *Atriplex longipes* is restricted to a very specialized habitat: relatively undisturbed, tall, salt marsh vegetation in the upper zones of estuaries on a silty substratum flooded with brackish water during the high spring tides. It is associated with *Aster tripolium* in stands dominated by *Juncus maritimus* and present at the margins of *Phragmites australis* stands.

MORPHOLOGY IN THE WILD

The plants mature by September and the aerial parts then disappear from the habitat. During seed maturation, the lower leaves change from succulent to thin, turn from green to yellow, and drop off. This process begins in the lowermost parts of the plant and progresses up to the top. In mature leaves separated from the plant, autolysis is very rapid. Rotting begins in the apical parts of the leaf and proceeds toward the central and basal parts.

Each bracteole pair has a very small point of attachment to the stem. At maturity the bracteoles readily break at this point separating from the plant and falling whenever the plant is disturbed.

TABLE 1. THE INFLUENCE OF SHADING, PRUNING, CROWDING, ON BRACTEOLE MORPHOLOGY AND BRACTEOLE STALK DEVELOPMENT IN *A. LONGIPES*

Treatment	Controls	Influence of treatment
SHADING Seedlings planted outdoors under dense growth of closely cultivated tall herbaceous annuals	Seedlings planted outdoors, well-spaced in an open, unshaded plot adjacent to the plot with the treated plants	Controls and treated plants did not differ significantly. Some plants in each group developed stalked bracteoles (stalks up to 5 mm long).
PRUNING Potted plants in greenhouse treated in the following way: Pruned at different developmental stages: (1) Before flowering (2) Immediately after flowering (3) During early fruit maturation Different parts pruned: (1) Central axis one-third up from the base (2) Side branches to various degrees	Potted plants unpruned, interspersed with the pruned plants on the same greenhouse bench	Controls and treated plants did not differ significantly. Some plants in each group developed stalked bracteoles (stalks up to 5 mm long).
CROWDING From 10 to 20 seedlings were planted in J.I. compost in 14 cm pots and allowed to grow to maturity without being repotted	Seedlings potted separately and repotted regularly into fresh J.I. compost every 2–3 weeks	Treated plants differed markedly from the controls and plants in other treatments: (1) Treated plants were approximately half the height of the controls (2) Bracteoles were morphologically similar to those on the parent plant (i.e. thin, foliose, reticulate-veined) (3) Stalks up to 10 mm long developed on numerous bracteoles

Table 2 compares the taxonomic characters of *A. longipes* with those of *A. prostrata*, the species with which it most frequently hybridizes.

In the field, two morphological variants were observed. These differ in size and habit: one is 1 m or more high with long (up to 50 cm) opposite lower branches and a straggling growth habit. It occurs at the margins of *Phragmites australis* stands. The other variant is 30–80 cm high with short (10–20 cm) alternate branches and an erect habit. It occurs in dense stands of *Juncus maritimus*. The influence of environment on the development of these two variants remains uncertain but observations on their cultivated offspring revealed that hybridization with *A. prostrata* was involved in all the larger ones.

MORPHOLOGY AND CULTIVATION

The cultivation results are summarized in Tables 1 & 3. The most important findings are that development of the bracteole stalk on *A. longipes* is subject to environmental modification, and that hybrids involving *A. prostráta* can be morphologically indistinguishable from *A. longipes*.

Stalk development on the bracteoles of *A. longipes* was affected by cultivation conditions. All the cultivated offspring had shorter stalks than their wild parents. Penpoll (77–43) plants, discussed above, showed no clear evidence of hybridization with *A. prostrata* and the cultivated plants came from seed selected from herbarium specimens exhibiting extreme bracteole stalk development (stalks up to 30 mm long). Despite this, 70% of the cultivated progeny of these plants with long-

TABLE 2. TAXONOMIC CHARACTERS OF *A. LONGIPES* AND *A. PROSTRATA* COMPARED IN BRITISH AND SCANDINAVIAN (GUSTAFSSON 1976) PLANTS MEASUREMENTS BASED ON CULTIVATED PLANTS ARE SHOWN IN BRACKETS

Characters	*A. longipes*	*A. prostrata*
LOWER LEAVES		
Outline	Elongate-triangular to rhombic	Deltoid-triangular to triangular hastate
Length/width ratio	1.2–1.5 British Isles (Cult.: 1.2–1.6) 1.3–3.5 Scandinavia	0.7–1.8 British Isles 0.9–2.0 Scandinavia
Base angle	100°–150° British Isles (Cult.: 120°–180°) 50°–145° Scandinavia	120°–250° British Isles 160°–230° Scandinavia
LARGEST BRACTEOLES		
Outline	Ovate-lanceolate	Triangular to triangular-ovate
Substance	Thin-herbaceous, foliaceous, never thickened	Thin herbaceous or slightly thickened
Lateral angles	Pointed, strongly developed	Rounded, not strongly developed
Basal stalks	Present, up to 30 mm long (Cult.: 0.5–5.0 mm long)	Absent
Venation	Prominent, forming a strongly reticulate pattern at the base	Obscure or slight throughout
Maximum length	25 mm British Isles 20 mm Scandinavia	7 mm British Isles 7 mm Scandinavia
BROWN SEEDS		
Diameter, mm	2.0–3.0 British Isles 1.7–2.7 Scandinavia	1.5–3.0 British Isles 1.5–2.7 Scandinavia
Radicle emergence	Basal to sub-basal	Sub-basal
Radicle direction	Out-pointing	Obliquely up-pointing

stalked bracteoles had entirely sessile bracteoles, and of the remaining 30%, few plants had bracteoles with stalks exceeding 2 mm, and none had bracteoles with stalks more than 3 mm long.

The failure of *A. longipes* to develop stalked bracteoles in cultivation was investigated experimentally. The different treatments and their influence on bracteole development are summarized in Table 1. Only crowding had any effect. The effect of crowding, by allowing numerous seedlings to grow to maturity without re-potting, produced plants that developed bracteoles with stalks up to 10 mm long. The bracteoles on these plants were morphologically much more similar to those on the parent plant than were the bracteoles on the controls and plants treated in other ways.

Height in the cultivated plants was extremely variable and not obviously related to the height of the plants from which they were derived. The lowermost branches in all the cultivated plants were long and spreading. In many cases they were up to two-thirds as long as the central axis.

Other differences between the wild plants and their cultivated progeny were in leaf-base angle, lower leaf morphology and the relative amounts of small, black seed compared to large, brown seed. Seed type proportion was examined only in the Penpoll population because plants from this

TABLE 3. RESULTS OF CULTIVATING *A. LONGIPES* SEEDS DERIVED FROM PLANTS COLLECTED IN KIRKCUDBRIGHTSHIRE, NORFOLK AND CORNWALL

Locality	Field No.	% Offspring showing *A. prostrata* characters	Length of bracteole stalks of parents (mm)	Length of bracteole stalks of offspring (mm)	% Offspring with all bracteoles sessile	Height of parents cm	Height of offspring cm
Palnure	75–97	60	5–20	1–3	65	c.70	80–150
Brancaster	76–15	38	5–15	1–5	54	c.90	40–50
Brancaster	76–18	30	5–15	1–5	50	c.90	40–90
Penpoll	77–43	0	5–30	1–3	70	45–55	70–150

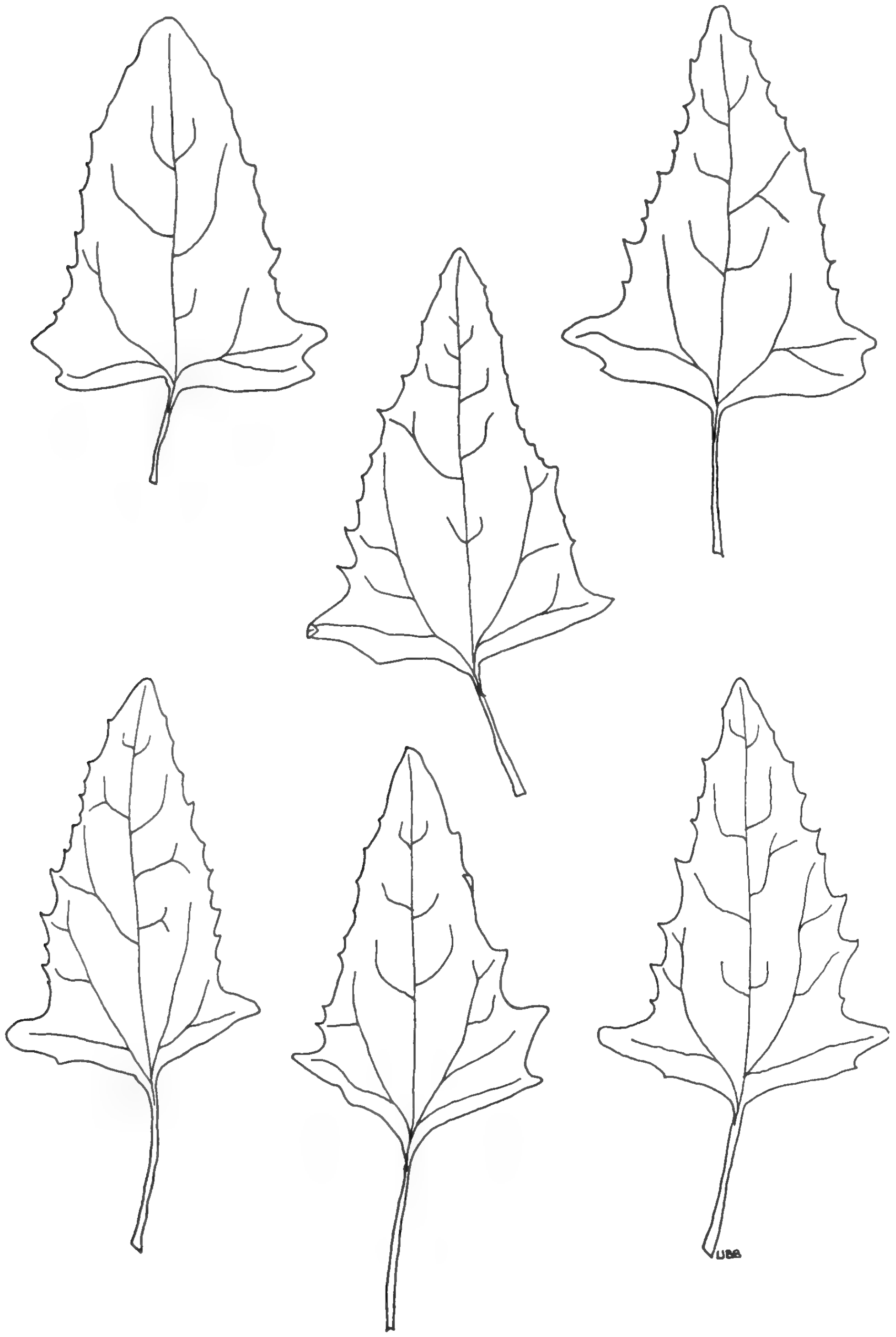


FIGURE 1. *A. longipes.* Variation in the lower leaves of cultivated plants derived from wild specimen (Penpoll 77–43).

population showed almost no evidence of hybridization with *A. prostrata.* The wild plants and their cultivated offspring are compared in Table 4 and variation in the morphology of the lower leaves of cultivated plants derived from Penpoll 77–43 is illustrated in Fig. 1.

HYBRIDIZATION: EVIDENCE FROM PROGENY TESTS

Hybridization with *A. prostrata*, not evident in the parents, showed up in the offspring. Some segregants were indistinguishable from *A. prostrata*, others exhibited in varying degrees the lower leaf and bracteole characters of that species. Two out of three populations showed evidence of

TABLE 4. DIFFERENCES BETWEEN WILD PLANTS OF *A. LONGIPES* (PENPOLL 77–43) AND THEIR CULTIVATED PROGENY

Character	Wild Plants	Cultivated progeny
Leaf base angle	100°–150°	120°–160°(–180°)
Amount black seed	35%	75%

introgression in the cultivated plants. In population 75–97 from Palnure, v.c. 73, 60% of the offspring had hybrid characters. The Palnure plants came from a habitat grazed and trampled by cattle. The habitat at Penpoll, v.c. 2, was by comparison relatively little disturbed. Plants cultivated from this population (77–43) did not exhibit distinctively hybrid characters but about 30% had truncate-based lower leaves suggesting some degree of introgression from *A. prostrata*.

The results of field and herbarium studies indicate that hybrid derivatives between *A. longipes* and *A. prostrata* and between *A. longipes* and *A. glabriuscula* are frequent on the coasts of the British Isles. One distinctive, stabilized variant of *A. longipes* × *A. prostrata* occurs on the northern and western coasts of Scotland and in Shetland. There it occupies exposed beaches where neither of the parents occur. In estuarine stands of *Agropyron pungens*, such as those bordering the River Avon near Bristol, v.c. 34, *A. longipes* × *A. prostrata* is often abundant. This same hybrid has been collected from inland salt marshes at Nantwich, v.c. 58, and Preesall, v.c. 60, and from waste ground in central Manchester.

DISCUSSION

MORPHOLOGY

The stalked bracteole, from which *A. longipes* takes its name and upon which much taxonomic emphasis (Aellen 1964) is often put, is by itself not a reliable character. Stalked bracteoles are characteristic of most hybrids involving *A. longipes*, and in the British Isles such hybrids are much more frequent than *A. longipes* itself. In cultivation, the hybrids may or may not produce stalked bracteoles while the species frequently produces only entirely sessile bracteoles. Growth density and nutrient status apparently influence the morphology and stalk development of *A. longipes* bracteoles, but the exact environmental factors remain obscure.

Gustafsson (1972) did not report any anomalies in bracteole stalk development in cultivated *A. longipes* in Scandinavia. His potting compost, however, was different. It was a mixture of two-thirds soil and one-third sand. His greenhouse conditions were also different and the populations from which his plants were derived were geographically distant from those in Britain.

The differences between the wild and cultivated plants in leaf-base angle and in the relative proportion of black to brown seeds may in part be due to factors other than introgression from *A. prostrata*. Leaf width frequently increases in *Atriplex* plants brought into cultivation. In species, such as *A. longipes*, that have basal lobes (between which the lamina width is measured) this increase is reflected in an increase in the basal angle. As in *A. glabriuscula*, the earlier-formed lower leaves measured in cultivated plants are largely absent in the wild specimens. Most of the lower leaves on *A. longipes* have dropped by the time the plants are sufficiently mature to be recognized. The later-formed leaves have a smaller leaf base angle.

The proportion of black to brown seed morphs is, in general, genetically fixed for a particular population (Hulme 1957). There is some evidence, however, that environmental conditions, especially light and day length, can alter this proportion slightly (Bassett & Crompton 1973; Jones 1971), but in the plants I cultivated between 1974 and 1978, the relative proportions of black to brown seeds did not change within a particular biotype. The ratio of black/brown seeds in *A. patula*, for example, remained unchanged in the progeny of a predominantly brown seeded population from Ontario that was cultivated alongside a predominantly black seeded population from Manchester. After two generations of cultivation under the same conditions, the Ontario biotype continued to produce about 70% large brown seeds, and the Manchester biotype continued to produce about 90% small black seeds (Taschereau 1979). In *A. longipes*, the black seeds mature earlier than the brown ones. The bracteoles within which they are contained are attached to the stalk at only a very small point and readily detach at maturity. The change in the relative proportion of black seeds to brown ones observed in the cultivated plants may be due to environmental influences or simply that fewer black seeds still remained on the wild plants at the time of collection.

HYBRIDIZATION

Atriplex longipes in the British Isles is known from but eight localities in six vice-counties (Taschereau 1985a). In all but one of the populations investigated in this study, the *A. longipes* plants proved to be of hybrid origin, involving to a greater or lesser extent *A. prostrata*. Although F_1

hybrids or their derivatives may look like either parent (Gustafsson 1973a; Taschereau 1985b), only the *A. longipes* morphological type was encountered. In addition to these cryptic hybrids, plants obviously intermediate between *A. longipes* and *A. prostrata* were frequent in all sites where *A. longipes* was found.

Hybrid derivatives between *A. longipes* and *A. glabriuscula* and between *A. longipes* and *A. prostrata*, so frequent on the coasts of Britain, have caused many identification problems. Since the presence of *A. longipes* was unknown until recently, its hybrid derivatives, when identified at all, were usually determined as *A. prostrata*, *A. glabriuscula* or the hybrid *A. glabriuscula* × *A. prostrata*. Inland forms of *A. longipes* × *A. prostrata*, frequently unlike either of the parent species, are also responsible for identification problems in *Atriplex*. Plants of this hybrid from inland salt marsh communities at Nantwich, v.c. 58, for example, are very distinctive and unlike the more abundant *A. prostrata* also present there. Hybrid plants, such as these, may be the basis of erroneous reports of *A. glabriuscula* from Cheshire salt marshes (Chapman 1960; Perring & Walters 1962; Lee 1975). Variants of *A. longipes* × *A. prostrata* with cuneate-based upper leaves are known from waste ground in central Manchester and probably occur elsewhere. Such plants could readily be confused as intermediates between *A. patula* and *A. prostrata* (Jones 1975b), the only native *Atriplex* species reported from inland localities.

Further investigation will probably reveal that hybrids between *A. longipes* and *A. prostrata* are even more frequent than reported here. In estuarine stands of *Agropyron pungens*, for example, the hybrids are known to occur, and according to Adam (1978), the *Atriplici-Agropyretum pungentis* association is one of the most widespread and extensive upper salt marsh communities of south-eastern England.

The rarity of *A. longipes* in Britain, in contrast to the abundance of its hybrids with *A. prostrata*, is probably due in large part to the modification of its natural habitat. The most important single determinant of salt marsh vegetation in England and Wales is past and present land use (Adam 1978). Few salt marsh habitats in Britain remain ungrazed, uncut or otherwise unutilized by man. The upper estuarine zone where *A. longipes* occurs has been heavily modified by man. Adam (1978) noted that few estuaries at present support extensive salt marshes in this zone and that all the British estuarine sites for which there are data show signs of obvious disturbance.

Hybridization in *A. longipes* is also favoured by the reproductive biology of this species. In Britain, as in Scandinavia (Gustafsson 1972), *A. longipes* exhibits a distinct protogyny. The pistillate flowers in the leaf axils extend a pair of receptive stigmas several days before the staminate flowers open and shed their pollen. Thus, the opportunity for cross pollination is increased.

The frequency of *A. longipes* hybrids and the data from experimental studies (Gustafsson 1973a) indicate that internal reproductive isolating mechanisms in this species are slight. The isolating mechanisms are primarily pre-zygotic. In Britain, *A. longipes* is sympatric only with *A. prostrata*. It is isolated from *A. praecox* except in south-western Scotland by differences in range, and from other related species by ecological barriers. There is some evidence of partial seasonal isolation between *A. longipes* and *A. prostrata* in Britain. The degree of overlap in flowering time cannot be determined because the flowering period of *A. longipes* is uncertain but, with few exceptions, *A. longipes* matures one to three weeks earlier than *A. prostrata*. In most British populations, *A. longipes* is in a state of advanced maturity by the first week in September when *A. prostrata* is just past flowering and is beginning to mature seed. By October, most *A. longipes* plants have disappeared from the habitat, leaving only the occasional, late-maturing plant.

In Scandinavia, differences in flowering time between *A. prostrata* and *A. longipes* result in absolute reproductive isolation in the Baltic region and partial isolation on the west coast. Grazing of the *A. longipes* habitat has been observed to induce late flowering in *A. longipes* and break down this seasonal isolating mechanism (Gustafsson 1973b). As discussed, few salt marsh habitats in Britain remain ungrazed, or otherwise undisturbed.

TAXONOMIC CONCLUSIONS

From the data presented above, it is clear that *A. longipes*, judged on the basis of interfertility, is less distinct as a species than are the other taxa comprising the *A. prostrata* group. Gustafsson (1972) expressed the view that *A. longipes* probably only deserves sub-specific rank within the *A. prostrata* group for the following reasons: 1) Great morphological similarity between it and the other taxa. 2) Spontaneous hybridization and introgression especially between *A. longipes* and *A. prostrata.* 3) Relatively high fertility values in spontaneous hybrids as well as in artificial crosses with all taxa in the group. In his taxonomic treatment, Gustafsson (1976), however, decided to rank *A. longipes* with *A. praecox*, making the latter a subspecies of *A. longipes*. In southern Scandinavia, hybridization between these two taxa is frequent and there are similarities in their morphology.

In Britain, the range of *A. praecox* does not overlap with that of *A. longipes* except in the extreme south-western part of Scotland. The taxa occupy very different habitats and hybrids between them are unknown. With *A. prostrata* the situation is quite different. Wherever *A. longipes* has been found, *A. prostrata* has been found nearby and hybrids between the taxa are commonly more frequent than *A. longipes* itself. If one considers the situation of *A. longipes* in Britain, excluding its behaviour in other geographical regions, then it should, both on genetic and morphological grounds, be ranked as a subspecies of *A. prostrata.*

As Stace (1975) noted, the species is by consensus a unit of practical value, morphologically discernable and, whenever possible, also having evolutionary significance. For practical, morphological, genetic and ecological reasons, I prefer at this time to maintain *A. longipes* at the species level. My reasons are as follows: firstly, *A. longipes* is morphologially distinct. It differs from *A. prostrata* in a number of clearly defined characters (Table 2). Throughout its range, *A. longipes* shows a consistent correlation between the taxonomic characters of the bracteoles and those of the lower leaves.

Secondly, *A. longipes* occupies a distinct ecological niche: it is restricted to tall vegetation of upper estuarine salt marsh communities. In this it is quite different from the broad-ranging *A. prostrata* which occurs in every halophytic habitat both coastal and inland and in addition produces numerous weedy biotypes that colonize waste places throughout Europe and North America.

Thirdly, despite the weak internal barriers to crossing and the generally high fertility of Gustafsson's (1973a) F_1 experimental hybrids, seed germination in his hybrids was highly reduced. Seed germination varied from 0 to 60% in all experimental crosses between *A. longipes* and *A. prostrata*, but in 20 out of 23 crosses, less than 30% germinated (Gustafsson 1973a). Seeds from natural hybrids in Scandinavia germinated poorly. In the majority of plants, seed germination did not exceed 30%. By contrast, seed germination in the parent taxa was between 80% and 90% in the majority of plants, and in none was it less than 40% (Gustafsson 1973b: 404).

Fourthly, the degree to which *A. longipes* hybridizes with *A. prostrata* is by itself not a sufficient criterion for uniting these species. The situation in which hybrids outnumber one or both of the parent species in a particular geographic region is not peculiar to *Atriplex*. It occurs, for example, in *Euphrasia*. In some regions, the parent species of a hybrid *Euphrasia* taxon have been hybridized out of existence (P. D. Sell 1977, pers. comm.). The genus *Crataegus* in North America is another example where hybrids may outnumber parents.

Finally, *A. longipes* provides the key to understanding much of the variation in the coastal taxa of the *A. prostrata* group in Britain. It hybridizes with *A. glabriuscula* as well as with *A. prostrata*. The resulting hybrid derivatives occur on virtually all coasts of the British Isles. They are ecologically and morphologically highly diverse and many of them behave as species. With the foundation laid by Gustafsson's experimental work on *A. longipes*, it is now possible to recognize these hybridogenous variants and to identify many of them. At this stage of our understanding, to reduce *A. longipes* to a subspecies or variety (Meijden 1982) of one of the taxa with which it hybridizes, obscures rather than clarifies its relationships to other members of the *A. prostrata* group.

ACKNOWLEDGMENT

I am grateful to B. U. Borluk, my friend and former colleague, for providing the excellent drawings of *Atriplex longipes*.

REFERENCES

ADAM, P. (1978). Geographical variation in British saltmarsh vegetation. *J. Ecol.*, **66**: 339–366.

AELLEN, P. (1964). *Atriplex* in TUTIN, T. G. *et al.*, eds. *Flora Europaea*, **1**: 95–97. Cambridge.

BASSETT, I. J. & CROMPTON, C. W. (1973). The genus *Atriplex* (Chenopodiaceae) in Canada and Alaska. III. Three hexaploid annuals: *A. subspicata*, *A. gmelinii*, and *A. alaskensis*. *Can. J. Bot.*, **51**: 1715–1723.

CHAPMAN, V. J. (1960). *Salt marshes and salt deserts of the world.* London.

GARVE, E. (1982). Die *Atriplex*-Arten (Chenopodiaceae) der deutschen Nordseeküste. *Tuexenia*, **2**: 287–333.

GUSTAFSSON, M. (1972). Distribution and effects of paracentric inversions in populations of *Atriplex longipes*. *Hereditas*, **71**: 173–194.

GUSTAFSSON, M. (1973a). Evolutionary trends in the *Atriplex triangularis* group of Scandinavia, 1. Hybrid sterility and chromosomal differentiation. *Bot. Notiser*, **126**: 345–392.

GUSTAFSSON, M. (1973b). Evolutionary trends in the *Atriplex triangularis* group of Scandinavia, 2. Spontaneous hybridization in relation to reproductive isolation. *Bot. Notiser*, **126**: 398–416.

GUSTAFSSON, M. (1974). Evolutionary trends in the *Atriplex triangularis* group of Scandinavia, 3. The effects of population size and introgression on chromosomal differentiation. *Bot. Notiser*, **127**: 125–148.

GUSTAFSSON, M. (1976). Evolutionary trends in the *Atriplex prostrata* group of Scandinavia, 4. Taxonomy and morphological variation. *Op. bot. Soc. bot. Lund.*, **39**: 1–63.

HEATH, J. & SCOTT, D. (1974). *Biological Records Centre instructions for recorders*, p. 16.Huntingdon.

HOLMGREN, P. K., KEUKEN, W. & SCHOFIELD, E. (1981). *Index Herbariorum*, 7th ed. Utrecht.

HULME, B. A. (1957). *Studies on some British species of* Atriplex. Ph.D. thesis, University of Edinburgh.

JONES, E. M. (1971). *Taxonomic and ecological studies in the genus* Atriplex. Ph.D. thesis, University of Oxford.

JONES, E. M. (1975a). Taxonomic studies of the genus *Atriplex* (Chenopodiaceae) in Britain. *Watsonia*, **10**: 233–251.

JONES, E. M. (1975b). *Atriplex*, in STACE, C. A., ed. *Hybridization and the flora of the British Isles*, pp. 185–186. London.

KENT, D. H. & ALLEN, D. E. (1984). *British and Irish herbaria.* London.

LEE, J. A. (1975). The conservation of British inland salt marshes. *Biol. Conserv.*, **8**: 143–151.

LIBBEY, R. P. (1977). *Atriplex longipes* Drej: a new Norfolk species. *Trans. Norfolk Norwich Nat. Soc.*, **24**: 75–77.

MEIJDEN, R. VAN DER (1982). Een nieuwe combinatie in *Atriplex*. *Gorteria*, **11**: 119.

PERRING, F. H. & WALTERS, S. M., eds (1962). *Atlas of the British flora.* London.

STACE, C. A., ed. (1975). *Hybridization and the flora of the British Isles.* London.

TASCHEREAU, P. M. (1977). *Atriplex praecox* Hülphers: a species new to the British Isles. *Watsonia*, **11**: 195–198.

TASCHEREAU, P. M. (1979). *Taxonomy of the genus* Atriplex *in Great Britain.* Ph.D. thesis, University of Manchester.

TASCHEREAU, P. M. (1985a). Taxonomy of *Atriplex* species indigenous to the British Isles. *Watsonia*, **15**: 183–209.

TASCHEREAU, P. M. (1985b). Hybridization in the genus *Atriplex* section *Teutliopsis* (Chenopodiaceae) *Watsonia*, **15**: (in press).

(*Accepted February 1984*)

Watsonia, **15**, 221–229 (1985)

The *Limonium auriculae-ursifolium* (Pourret) Druce group (Plumbaginaceae) in the Channel Isles

M. J. INGROUILLE

Department of Botany, Birkbeck College, Malet Street, London, WC1E 7HX

ABSTRACT

The history of the investigation of the *Limonium auriculae-ursifolium* group (Plumbaginaceae) in the Channel Isles is related. Evidence is presented, from a cultivation experiment, that shows the presence in the islands of two variants in this group, *L. auriculae-ursifolium* sensu stricto and **L. normannicum** Ingrouille **sp. nov.**

INTRODUCTION

Limonium auriculae-ursifolium (Pourret) Druce was first discovered in the Channel Isles in August 1900 (Salmon 1901), growing at St Esquère Bay on the eastern tip of Alderney (GR WA 607.088, M.O.D. 1:10560 Alderney map (1966)). Later it was found in three places on the northern coast of Jersey (Fig. 1): at Rouge Nez, near Crabbe (Attenborough 1916), at Plémont Point (Attenborough 1918) and at Ronez Point in 1919 (Attenborough 1920) (G.R. 588.558, 562.567, 518.572 respectively, Official States of Jersey 1:25000 map (1981)).

The Alderney Sea-Lavender has long been known from the Atlantic coast of France in Dépts Morbihan, Loire-Atlantique and Gironde (Lloyd 1844). It was first described from the Mediterranean coast of France, from Guissan near Narbonne, as *Statice auriculae-ursifolia* Pourret (Pourret 1788). It was later found in Spain and Portugal (Boissier 1848), in the Balearic Islands (Pignatti 1960) and on the northern coast of France opposite the Channel Isles (Salmon 1902).

The same species was described from L'Isle Saint Lucie, adjacent to the original type locality, as *Statice lychnidifolia* Girard (Girard 1842), and for a long time it was this synonym which was used in Floras. The earlier name of *L. auriculae-ursifolium* was not properly adopted until 1928 (Druce 1928).

It was Boissier (1848) who first formally recognized the variation present within *L. auriculae-ursifolium* by describing a var. *corymbosa* from southern Spain (Cádiz and Málaga) and from the western coast of France. Recently Erben (1978) described part of Boissier's variety, i.e. those plants from southern Spain and Portugal, as a new species, *L. algarvense* Erben. He also recorded a variant from the northern Atlantic coast of France, which required further investigation.

C. E. Salmon (1901) was quick to identify the Alderney Sea Lavender as Boissier's var. *corymbosa* (*L. lychnidifolium* var. *corymbosum* (Boissier) C. E. Salmon), by its subcorymbose habit, and extended Boissier's rather sketchy description from Alderney material.

It was Frère Louis Arsène who first noted the differences between plants from different places on Jersey (Arsène 1930). He described the different branching pattern and smaller spikelets of the plants from Plémont Point and the congested panicle of plants from Ronez Point. In a note on one herbarium specimen (**JSY**), he suggested that the plants from Plémont Point might be hybrids between the Ronez Point plants and Rock Sea Lavender, *L. binervosum* (G.E.Sm.) C. E. Salmon (*L. occidentale* (Lloyd) O. Kuntze), which is also found at Plémont Point. At this time C. E. Salmon was rather diffident about determining the Plémont Point plants as var. *corymbosum* but had no reluctance in labelling Ronez Point plants as such.

In recent years the populations at Ronez Point and that from Rouge Nez (which resembles the Plémont Point variant) have been searched for without success. The Ronez Point population was adjacent to, or in, a quarry used by the German army during the Second World War, from which stone was transported by rail to build the fortifications of St Ouen's Bay. It was during the war that a colony of *L. lychnidifolium* var. *corymbosum* appeared along St Ouen's Bay, probably founded by

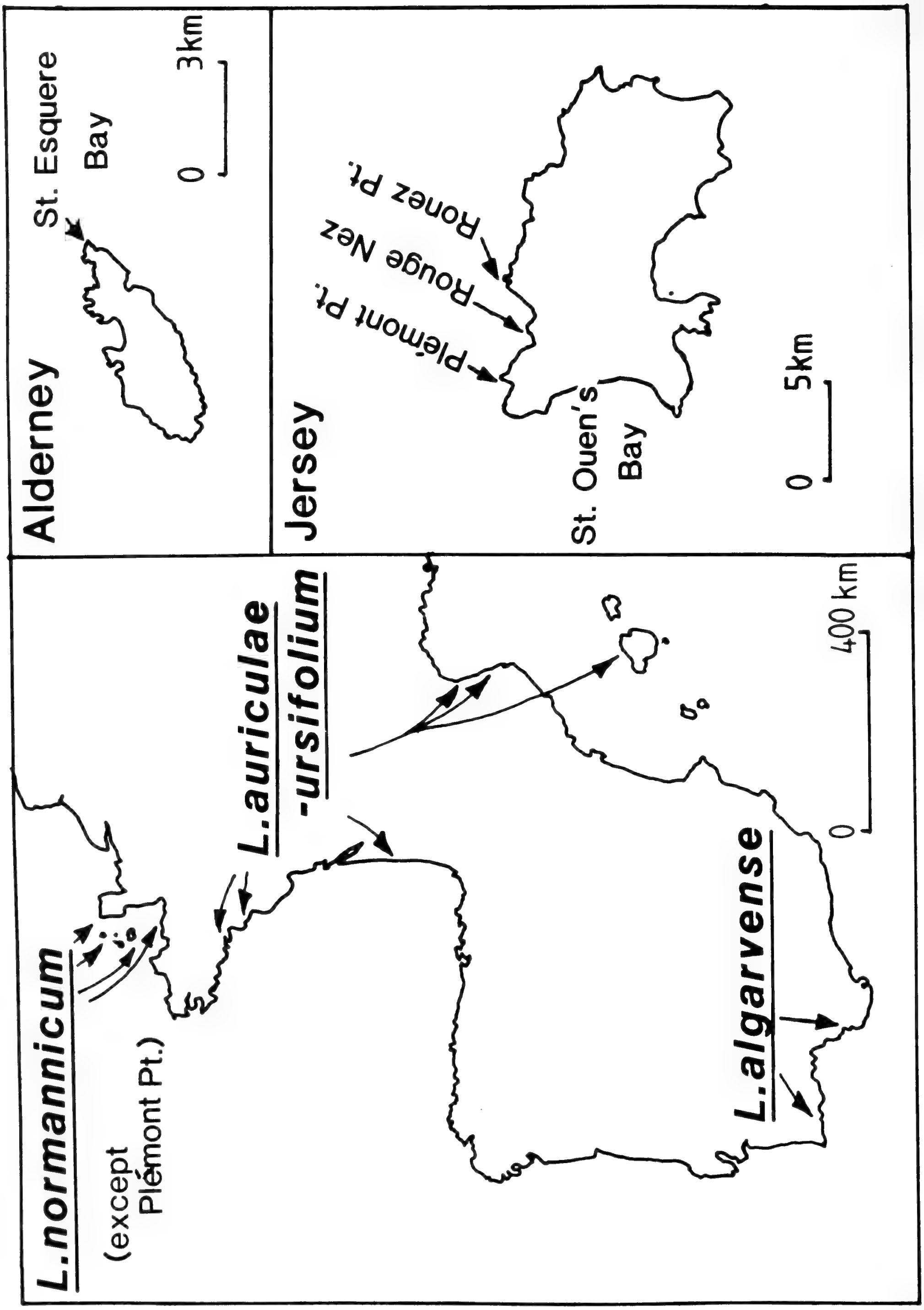


FIGURE 1. Distribution of *Limonium auriculae-ursifolium* agg. in western Europe and in the Channel Isles.

seed from Ronez Point plants. At present, this colony is by far the largest in the Channel Isles, numbering many hundreds of plants, and is especially abundant at the White Guard House (La Caumine de Mary Best) and at El Tico café (GR 564.521 and 564.518, Official States of Jersey 1:25000 map (1981)).

Here it grows on stabilized dunes, with *Catapodium marinum* (L.) C. E. Hubbard, *Cynodon dactylon* (L.) Pers., *Ammophila arenaria* (L.) Link, *Plantago coronopus* L., *Armeria maritima* (Mill.) Willd., *Honkenya peploides* (L.) Ehrh. and *Salicornia* sp. The colony at St Esquère Bay, Alderney, is smaller, numbering tens of plants. Here it grows with *L. binervosum* (G. E. Sm.) C. E.Salmon on low rocks beside the sea.

The only other surviving colony of *L. auriculae-ursifolium* agg. in the Channel Isles is that at Plémont Point which numbers only about 10 individuals, though each of these numbers from few to tens of rosettes. The colony grows in rock crevices on the side of a bare granite gully, with *Crithmum maritimum* L.

This paper raises to specific rank the northern French and Channel Isles plants referred to var. *corymbosum* by Salmon, and reports the results of cultivation of plants from the three present-day Channel Isles populations.

MATERIALS AND METHODS

Cultivated material was grown in a mixture of equal parts of John Innes No. 1 compost, coarse sand and grit, in 7.5 cm pots. Plants were kept in an unheated glasshouse at Leicester University until November 1981 and thereafter in a cold frame at Birkbeck College in London. Details of the cultivated material are given in Table 1.

TABLE 1. CULTIVATED MATERIAL OF *LIMONIUM AURICULAE-URSIFOLIUM* AGG. FROM THE CHANNEL ISLES

Site	Collector and date	Origin	Date sampled for measurements
Plémont Point, Jersey	F. Le Sueur, September 1979	Collected as seed	June 1983
St Ouen's Bay, Jersey	M. Ingrouille, May 1980	Collected as cuttings	June 1981
St Esquère Bay, Alderney	Unknown, cultivated at Leicester since 1978	Collected as seed	June 1981

Mitotic preparations were made from root tip squashes. Root tips were collected at midday, pretreated for 3 hours with hexachlorocyclohexane, fixed in 3:1 ethanol:glacial acetic acid, squashed, and stained with aceto-carmine.

TAXONOMIC DESCRIPTION

Limonium normannicum Ingrouille, **sp. nov.** (Fig. 4; A1, A2)
HOLOTYPUS: Rocks, Alderney, Channel Isles, 1900, *C. R. P. Andrews* (**BM**, **herb. J. Groves**).
PARATYPI: On seashore rocks, Alderney, Channel Isles, 27.7.1901, *E. W. Marquand* (**BM**, **herb. J. Groves**); Ronez Point, Jersey, 8.8.1919, *Père Morin* (**JSY**); 2.9.1925, *Frère Ariste* (**JSY**); St Ouen's Bay, Jersey, 12.9.1950, *Frère L. Arsène* (**JSY**).
Synonyms: *Statice lychnidifolia* Girard var. *corymbosa* Boiss. (1848) in DC. *Prodr.* **12**. pro parte. *Limonium lychnidifolium* (Girard) O. Kuntze var. *corymbosum* (Boissier) C. E. Salmon (1901) *J. Bot., Lond.* **39**: 192–195.

Planta perennis glabra oligocaulis. Folia basalia per anthesis persistentia usque ad 120 mm longa et 24 mm lata, late obovata-spathulata, obtusa; lamina auriculae-ursi similis in petiolum usque ad 6 mm latum sensim attenuata, herbacea, subtus 5-nervata vel plus, supra laevis. Folia caulina inferiora anguste triangulari-acuminata, squamata usque ad 10 mm vel infirma usque ad 25 mm longa. Caules usque ad 25 cm alti, nonnunquam in parte inferiore ramosi, erecti, recti vel in parte ramosa flexuosi. Inflorescentia subcorymbosa. Spicae usque ad 20 mm longae, densissime (spiculae 7–8 per cm dispositae) secundae vel biseriales. Bractea inferior 2.6–4.2 mm longa et 2.6–4.0 mm lata, late ovata, crassiuscula, margine membranacea. Bractea media 2.1–3.4 mm longa et 1.4–2.8 mm lata, biloba, membranacea. Bractea superior 4.5–6.9 mm longa et 3.5–5.8 mm lata, elliptica vel obovata, rotunda, margine late hyalina, parte centrali crassa, apice acuminata, acumine marginem hyalinum non contingente. Calyx 4.1–6.3 mm longus, rectus, infundibuliformis, tubo quam limbo 1.5–1.6-plo longiore, in parte inferiore piloso, calycis lobis transverse late semi-ellipticis, plicatis. Corolla infundibuliformis, petalis 6.2–7.4 mm longis × 2.1–2.8 mm latis, cuneatis, emarginatis, pallide violaceis.

Plant perennial, glabrous, (except for calyx) with one scape (occasionally more) to each rosette, smooth. Rosette leaves 35–120 × 11–24 mm, broadly obovate-spathulate with an obtuse (acute) apex, mucronate, with mucro to 1 mm long; lamina 0.3–0.5 × length and 3.0–6.0 × width of petiole, convex laterally, concave longitudinally; petiole broadly winged, with at least two obvious parallel veins on either side of the midrib. Leaves grey-green, glaucous, rigid, held erect, persisting at time of flowering. Scape up to 25 cm but usually 5–20 cm, erect, robust, branching from the lowest node or several nodes above; stem straight becoming zig-zag in the branched portion, subcorymbose; scape diameter up to 2.5 mm. Scape scale leaves narrowly triangular (3–10 mm) with an acute apex, the lowest often much larger (up to 25 mm long). Branches strong (diameter up to 2.2 mm), arranged regularly alternately or more often spirally, often with secondary branches arising at each node; branches below longer than those above, up to 3/4 total length of scape, or rarely the lowest branch short (up to 3 cm) and weak (diameter less than 1 mm); branching at 30–45°. Spikes concentrated in upper quarter to third of scape, congested, spreading or recurved, up to 20 mm, usually 6–15 mm long, with 2–13 spikelets; long spikes often with a much shorter spike arising at the same node; pedicels very short, up to 4 mm. Spikelets very crowded, 1–3 flowered, 7–8 per cm. Outer bract widely ovate, slightly acuminate, (2.6)3.0–4.0(4.2) × (2.6) 2.8–3.2(4.0) mm, herbaceous with a broad hyaline margin, but together sometimes forming a short cusp. Middle bract asymmetrical, 2-lobed, (2.1)2.2–2.9(3.4) × (1.4)1.6–2.5(2.8) mm, each lobe ovate, hyaline, the larger lobe with a herbaceous vein. Inner bract widely elliptic-obovate, (4.5)4.9–5.6(6.9) × (3.5)3.8–5.0(5.8) mm, with a broad hyaline margin, 0.7–1.0 mm wide; inner herbaceous region obovate, with the midrib slightly excurrent and forming a point up to 0.5 mm. Bracteoles usually 1, of variable size, with 1 green vein. Calyx (4.1)4.8–5.5(6.3) mm infundibuliform; basal portion (tube) herbaceous, pubescent-pilose, with 5 strong ribs excurrent into chartaceous upper region (limb); ribs terminating well below the base of the calyx teeth; tube 0.6–0.7 × length of calyx; teeth 0.5–1.0 mm long triangular–semi-elliptic, acute; pedicels 0.3–0.5(0.7) mm. Petals (6.2)6.5–7.2(7.4) × 2.1–2.5(2.8) mm, pale violet, cuneate, emarginate. Seed smooth, reddish, 1.5–2.0 mm long, narrowly ovate. Incompatibility morph 'Papillate', 'B' pollen. Chromosome number: 2n=25 (material from Saint Ouen's Bay, Jersey and St Esquère Bay, Alderney).

Distribution: CHANNEL ISLES: Alderney (St Esquère Bay); Jersey (St Ouen's Bay, Ronez Point); FRANCE: Dépt. Île et Vilaine (near St Malo) (Erben 1978); Dépt. Manche (Cherbourg, Surville (Erben 1978), Cartaret, Portbail (Salmon 1902)).

This taxon differs from *L. auriculae-ursifolium* sensu stricto in the following characters: leaves more usually with an obtuse rather than a rounded-obtuse apex; scape shorter, usually less than 20 cm tall, crowded, subcorymbose, with branches often arising from low down and arranged spirally; spikes larger, more swollen-looking and crowded together, recurved; bracts and calyx larger; incompatibility morph 'Papillate' stigma/'B' pollen rather than 'Cob' stigma/'A' pollen.

RESULTS AND DISCUSSION

Measurements of cultivated plants are shown in Table 2. Measurements of herbarium material from the 'extinct' colonies of Rouge Nez and Ronez Point are included for comparison.

TABLE 2. MEAN DIMENSIONS (±95% CONFIDENCE LIMITS) OF SPIKELET PARTS, IN MM, OF COLONIES OF *LIMONIUM AURICULAE-URSIFOLIUM* AGG. FROM THE CHANNEL ISLES

		St Esquère Bay (Alderney)		St Ouen'sBay (Jersey)		Ronez Pt (Jersey)	Plémont Point (Jersey)		Rouge Nez (Jersey)
		wild	cultivated	wild	cultivated	wild	wild	cultivated	wild
Outer	Length	2.6±0.4	2.7±0.8	3.7±0.6	3.2±0.9	3.3±0.7	2.2±0.3	2.2±0.1	2.3±0.4
bract	Width	2.7±0.2	2.9±0.5	3.3±0.3	3.1±0.9	3.2±0.7	1.9±0.3	2.0±0.3	2.1±0.4
		n=12	n=12	n=11	n=10	n=12	n=8	n=8	n=10
Middle	Length	2.3±0.2	2.2±0.3	3.0±0.5	2.7±0.2	2.5±0.4	2.0±0.2	2.1±0.3	2.1±0.2
bract	Width	1.9±0.3	1.9±0.4	2.3±0.6	2.3±0.2	2.1±0.6	1.5±0.2	1.4±0.1	1.6±0.2
		n=5	n=7	n=10	n=10	n=8	n=6	n=6	n=8
Inner	Length	5.2±0.5	4.8±0.5	5.7±0.4	5.3±1.2	5.4±0.9	4.2±0.5	3.9±0.6	4.5±0.5
bract	Width	4.2±0.6	4.4±0.4	4.7±0.4	4.9±1.3	5.2±0.6	3.6±0.4	4.0±0.7	4.2±0.3
		n=10	n=10	n=12	n=10	n=10	n=9	n=7	n=10
Calyx	Length	5.5±0.3	5.2±0.4	6.0±0.7	5.1±0.4	5.8±0.3	4.3±0.7	4.1±0.4	4.8±0.5
		n=9	n=9	n=10	n=10	n=10	n=4	n=6	n=6
Petals	Length	6.7±0.6	7.1±0.4					6.8±0.6	
								n=4	
	Width	2.3±0.2	2.5±0.4					1.9±0.2	
		n=10	n=10					n=12	

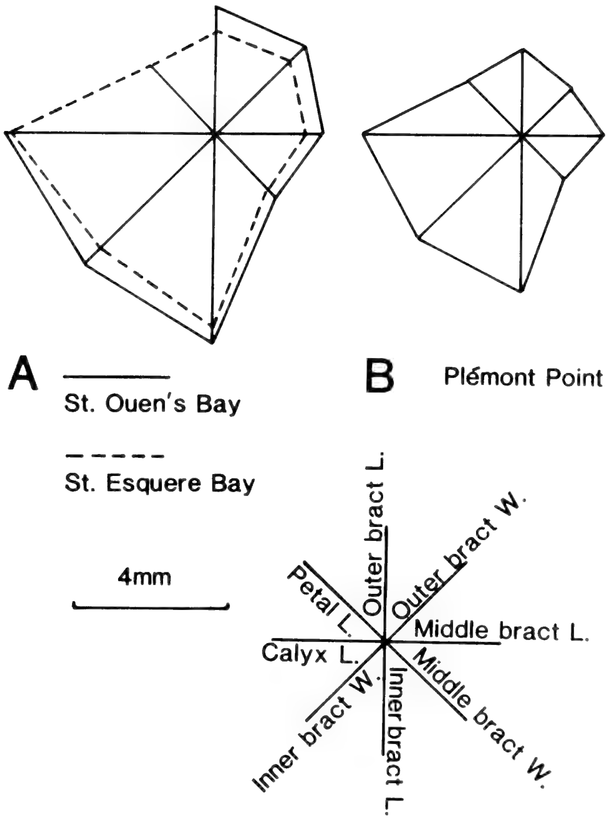


FIGURE 2. Polygonal graphs of eight spikelet characters of: A. *Limonium normannicum*, B. *L. auriculae-ursifolium*. L=length W=width.

A number of differences are apparent between the St Esquère Bay and St Ouen's Bay colonies (*L. normannicum*) and the colony from Plémont Point. The latter has much the smaller bracts (Fig. 2) of *L. auriculae-ursifolium* sensu stricto. It is, however, the presence in these plants of the 'A'/Cob morph characteristic of *L. auriculae-ursifolium* from further south which identifies this population as this species. The presence of different incompatibility morphs within the *L. auriculae-ursifolium* group was first noted by Baker (1953). Sexual species of *Limonium* such as the related *L. ovalifolium* (Pourret) O. Kuntze from Portugal and western France are dimorphic (Fig. 3). The presence of a single self-incompatible morph in each *L. auriculae-ursifolium* group colony preventing sexual reproduction indicates its agamospermous nature which is confirmed by the presence of a maintained aneuploid, triploid chromosome number of 2n=25. Baker (1953) demonstrated agamospermy in plants from Jersey by a continual emasculation experiment on isolated plants.

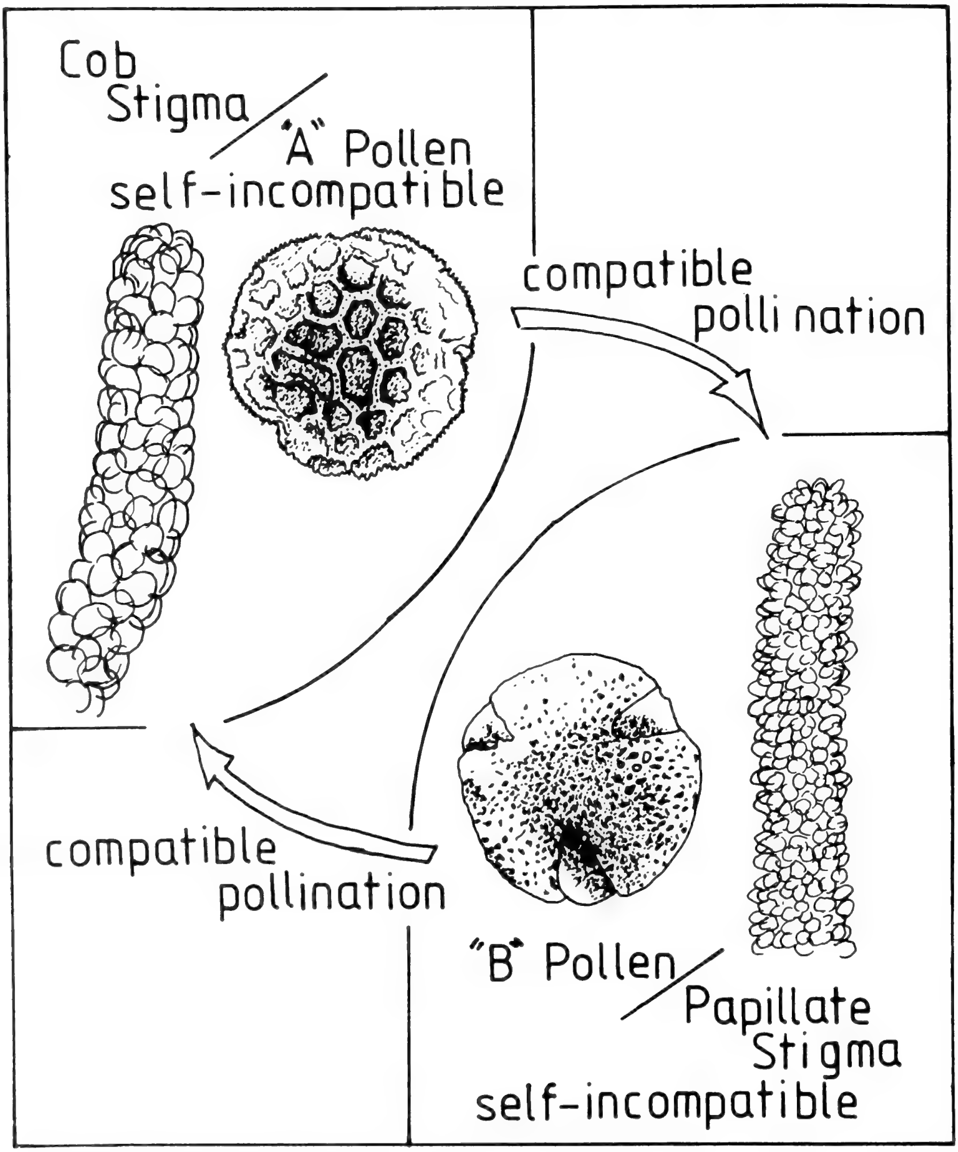


FIGURE 3. Sexual incompatibility morphs in *Limonium*.

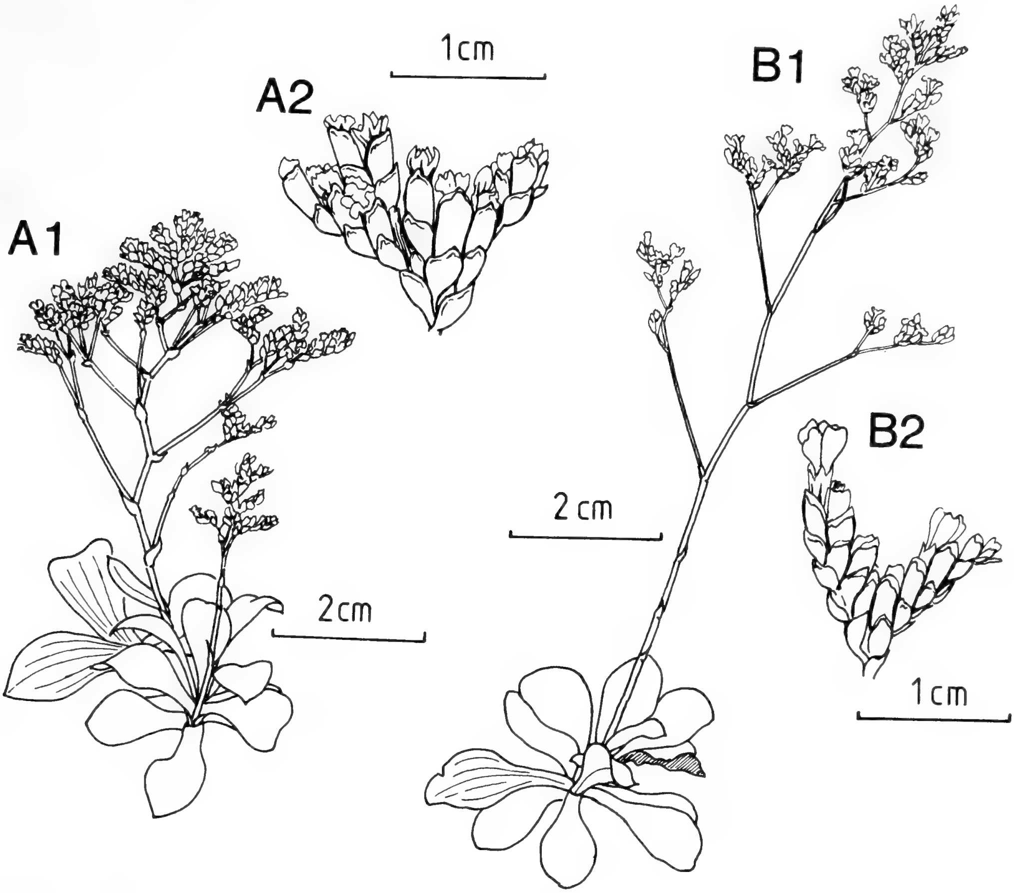


FIGURE 4. Whole plants of: A1. *Limonium normannicum* (St Esquère Bay, Alderney); B1. *Limonium auriculae-ursifolium* (Plémont Point, Jersey). Portion of scape of: A2. *L. normannicum*; B2. *L. auriculae-ursifolium*. Drawn from plants cultivated in London.

Within the group, the 'B'/Papillate incompatibility morph is otherwise present only in *L. algarvense*. It provides a single unambiguous character which argues very strongly for the recognition of *L. normannicum* as an agamospermous species distinct from *L. auriculae-ursifolium*. *L. normannicum* is readily distinguished in several other respects, not least its subcorymbose habit and fatter spikes (Fig. 4, Table 3). *L. normannicum* is much closer to *L. algarvense*, with which it shares both its incompatibility morph and subcorymbose habit but from which it differs by its much larger outer bracts.

Baker (1953) hypothesized that different variants of the *L. auriculae-ursifolium* group had arisen as hybrids between the related diploid sexual species *L. ovalifolium* with $2n=16$ and the agamospermous *L. binervosum* (G. E. Smith) C. E. Salmon group with $2n=27$ or 35. According to Baker the $2n=25$ of *L. auriculae-ursifolium* is obtained by adding a haploid *L. ovalifolium* complement to a haploid *L. binervosum* complement ($8+17=25$). Different incompatibility morphs and morphological variants can then be explained by their polytopic origin.

The difficulty of determining the hybridity of the *L. auriculae-ursifolium* group on morphological criteria, i.e. between *L. binervosum* and *L. ovalifolium*, arises from the great variability of the *L. binervosum* group. The latter consists of eleven species and many taxa of lesser rank (Ingrouille & Stace 1985). One could probably construct by the careful choice of characters a hybrid index which might prove intermediacy or non-intermediacy. However *L. auriculae-ursifolium* is very much

TABLE 3. CHARACTERS OF SPECIES OF *LIMONIUM AURICULAE-URSIFOLIUM* AGG. AND *L. OVALIFOLIUM*. MEASUREMENTS (RANGE IN BRACKETS) IN MM

		L. auriculae-ursifolium	*L. normannicum*	*L. algarvense*	*L. ovalifolium*
Shape of inflorescence		Obtrulloid	Subcorymbose	Subcorymbose	Subcorymbose-obtrulloid
Outer bract	Length	(1.8)1.9–2.4(2.9)	(2.6)3.0–4.0(4.2)	(1.7)1.9–2.3(2.6)	0.9–1.6(1.8)
	Width	(1.6)1.8–2.3(2.6)	(2.6)2.8–3.2(4.0)	(1.9)2.1–2.6(2.8)	1.0–1.5(2.0)
Middle bract	Length	(1.5)1.9–2.3(2.4)	(2.1)2.2–2.9(3.4)	(1.7)1.9–2.3(2.4)	(1.1)1.3–1.7(2.0)
	Width	(1.4)1.6–1.7(2.1)	(1.4)1.6–2.5(2.8)	(1.4)1.6–2.0(2.2)	(0.8)1.0–1.2(1.6)
Inner bract	Length	(3.7)4.2–5.6(5.7)	(4.5)4.9–5.6(6.9)	(4.2)4.5–5.1(5.3)	(2.7)3.0–3.7(4.0)
	Width	(3.4)3.6–4.4(4.9)	(3.5)3.8–5.0(5.8)	(3.6)4.0–4.8(5.0)	(2.7)3.1–3.5(4.1)
Calyx	Length	(3.8)4.0–4.6(5.5)	(4.1)4.8–5.5(6.3)	(4.0)4.2–4.8(5.2)	(3.2)3.8–4.1(4.4)
Petal	Length	(6.0)6.5–7.0(7.4)	(6.2)6.5–7.2(7.4)	6.0–7.5	(4.7)5.5–6.8
	Width	1.9–2.6	2.1–2.5(2.8)	2.2–2.6	(1.5)1.6–1.9
Incompatibility morph		Monomorphic 'A'/Cob	Monomorphic 'B'/Papillate	Monomorphic 'B'/Papillate	Dimorphic 'A'/Cob, 'B'/Papillate
Chromosome no.		2n=25	2n=25	2n=25	2n=16
Geographical range		Western and Mediterranean France, Balearic Islands	Northern France, Jersey and Alderney	Southern Portugal, southern Spain	Western France, western Portugal, Morocco

closer morphologically to *L. ovalifolium* than to *L. binervosum*. In a numerical taxonomic study of *Limonium* species, which will be reported elsewhere, *L. ovalifolium* clustered with the *L. auriculae-ursifolium* group first and then with a larger group of other agamospermous and sexual species before the *L. binervosum* group. *L. ovalifolium* could legitimately be regarded as the sole sexual member of the *L. auriculae-ursifolium* group (Table 3).

Variation between members of the group may have arisen by asexual means, by the accumulation of somatic and chromosomal mutations, as is almost certainly the case in the *L. binervosum* group (Ingrouille & Stace, 1985). The presence of different incompatibility morphs may be the result of autosegregation. There is certainly some evidence for variation within each species in the *L. auriculae-ursifolium* group in the Channel Isles. Plants from Alderney have slightly smaller spikelets than plants of *L. normannicum* from Jersey. The petals of *L. auriculae-ursifolium* from Plémont Point are narrower than those from further south.

The presence of *L. auriculae-ursifolium* sensu stricto at Plémont Point, geographically extremely isolated from French material, is very interesting and makes the conservation of this tiny colony very important.

ACKNOWLEDGMENTS

I would like to thank all those in the Channel Isles who helped me with my work, especially Mrs Frances Le Sueur. Work was carried out in part at the Botany Department, University of Leicester, supported by an SERC studentship. The Latin was checked by Dr R. R. Mill, Royal Botanic Gardens, Edinburgh. My thanks also go to Dr C. A. Stace for his guidance of this research.

REFERENCES

Arsène, F. R. L. (1930). *Limonium lychnidifolium*. *Rep. botl Soc. Exch. Club Br. Isl.*, **1929**: 231.
Attenborough, T. W. (1916). *Limonium lychnidifolium*. *Rep. botl Soc. Exch. Club Br. Isl.*, **1915**: 494.
Attenborough, T. W. (1918). *Limonium lychnidifolium*. *Rep. botl Soc. Exch. Club Br. Isl.*, **1917**: 116.

ATTENBOROUGH, T. W. (1920). *Limonium lychnidifolium. Bull. a. Soc. Jersiaise*, **45**: 165.

BAKER, H. G. (1953). Race formation and reproductive method in flowering plants. *Symp. Soc. Exp. Biol.*, **7**: 114–143.

BOISSIER, E. P. (1848). Plumbaginaceae, in DE CANDOLLE, A. P. *Prodr. Syst. Nat. Reg. Veg.*, **12**: 617–696. Paris.

DRUCE, G. C. (1928). *British plant list*, p. 77. Arbroath.

ERBEN, M. (1978). *Limonium* in Sudwestmediterranen. *Mitt. Bot. München*, **14**: 361–631.

GIRARD, F. DE (1842). Description de quelques espèces nouvelles de *Statice* appartenant à la flore de la France. *Ann. Sci. Nat. (Paris)*, Ser. 2, **17**: 18.

INGROUILLE, M. J. & STACE, C. A. (1985). The *Limonium binervosum* (G. E. Smith) C. E. Salmon aggregate in the British Isles. *Bot. J. Linn. Soc.*, (in press).

LLOYD, J. (1844). *Flore de la Loire-Infèrieure.* Nantes.

PIGNATTI, S. (1960). Studi sulla flora vegetazione dell' Isola di Mallorca (Baleari), I. *Limonium* della flora balearica (supplemento). *Arch. Bot.*, **36**: 206–210.

POURRET, P. A. (1788). *Statice auriculae-ursifolia. Mem. Acad. Sci. Toulouse* **3**: 330.

SALMON, C. E. (1901). *Limonium lychnidifolium* var. *corymbosum. J. Bot., Lond.*, **39**: 192–195.

SALMON, C. E. (1902). *Limonium. Rep. botl Soc. Exch. Club Br. Isl.*, **1901**: 56.

(*Accepted March 1984*)

Watsonia, **15**, 231–236 (1985)

What are the criteria for presuming native status?

D. A. WEBB

School of Botany, Trinity College, Dublin 2

ABSTRACT

Decisions on native or alien status of British or Irish plants are based all too often on inappropriate criteria, on irrelevant emotions such as local patriotism, or misinterpretation of fossil data, or on an uncritical acceptance of earlier opinions. Neither abundance nor 'looking wild' can be accepted as firm evidence of native status. The frequent practice of treating long-established aliens as equivalent to natives gives rise to confusion in discussions of phytogeography or quaternary history; the former may be hard to distinguish from natives, but they are aliens none the less. Eight criteria are here suggested; very seldom will any one of them give a definite answer, but if several provide circumstantial evidence pointing in the same direction it is reasonable to accept it as decisive. The criteria suggested are: fossil evidence; historical evidence; habitat; geographical distribution; ease of known naturalization elsewhere; genetic diversity; reproductive pattern; supposed means of introduction. A list is presented of species given without qualification as natives in the *Flora of the British Isles* (2nd ed.) by Clapham, Tutin and Warburg, whose status appears to the author to be subject to considerable doubt. The list is not exhaustive.

THE PROBLEM

Most Floras make some attempt to distinguish between native and introduced species, though some of them do so rather half-heartedly. But their authors seldom disclose the evidence which has led them towards their decision, and all too often it would appear that the assignment has been made either by copying uncritically from earlier works or on essentially intuitive grounds. I would like to suggest that the matter deserves more careful and more dispassionate consideration than it usually receives.

It would seem, moreover, that some authors interpret the term 'native' as synonymous with 'long-established'. Tutin (1962) for example, says of *Eryngium campestre** "Native . . . probably introduced in some localities, but certainly established at Plymouth before 1670". Apart from the fact that the small print in Martin & Fraser (1939) suggests that there is room for doubt as to whether the 1670 station is the same as any in which the plant grows today, one must infer that he regards "established since 1670" as different from "introduced". On the other hand Healy & Edgar (1980), discussing the flora of New Zealand, write that "for some species there must always be doubt as to whether they are truly indigenous or adventive . . . a certain proportion of plants considered native to New Zealand could have been quite recent immigrants, especially species whose seeds can be carried by wind or distributed by birds". Since it seems fairly certain that most of the non-endemic species of New Zealand must have arrived in quaternary or late tertiary times by some such methods there is little to be gained by calling a species that so arrived in prehistoric times 'indigenous' and one that arrived by the same means in historic times 'adventive'. This is not to say that great interest may not attach, in the case of some species, to the date of arrival in the territory in question; but if we are to make any sense of biogeography or quaternary history, we must surely recognize that whereas the agents of dispersal that have been operating for millennia are still operating, man has recently become an agent for dispersal on quite a different scale. While he was still a hunter or food-gatherer he may well have shifted some seeds from one place to another, but only in the same manner as a bear or an ape. But as soon as he began to herd flocks and to till the ground his impact on plant-geography suddenly increased enormously, and he ceased to be in any ordinary sense a part of nature but became a phenomenon sui generis.

*Nomenclature throughout follows Tutin *et al.* (1964–80).

In this paper I am concerned with the flora of Britain, and to some extent of Ireland, and I therefore define a native plant as one which evolved in these islands or which arrived there by one means or another before the beginning of the neolithic period, or which arrived there since that date by a method entirely independent of human activity. An alien, on the other hand, is one which reached the British Isles as a consequence of the activities of neolithic or post-neolithic man or of his domestic animals.

The more recent the introduction the easier it is, of course, to be sure of alien status, and it must be frankly admitted that for many species a decision between indigenous status and introduction as a weed of neolithic crops may be difficult or perhaps impossible. Some botanists, therefore, distinguish between 'palaeosynanthropic' and 'neosynanthropic' plants, and for most purposes lump the former with natives. The dividing line between the two is put at about A.D. 1550 when, as a result of the voyages of discovery, plants from America and eastern Asia came flooding in on an unprecedented scale. But this practice, although it saves many question marks and qualifications, obscures an important difference. If we are trying to work out the laws of plant-geography, *Agrostemma githago* must be as firmly classified as alien as is *Buddleja davidii.*

If I challenge a fellow-botanist who asserts that a plant considered by some to be alien is really native, and ask him for his evidence, he is apt to reply either "Well, there are such masses of it" or else "Well, it *looks* native at such-and-such a place". A glance at *Rhododendron ponticum* in the Killarney woods or at *Senecio squalidus* by the railway-lines of Yorkshire is enough to dispose of the former reply. The unreliability of the latter can be neatly illustrated by two passages from More (1868a,b), writing in the *Journal of Botany*. On p. 255, this leading Irish floristic botanist of the day, and a careful observer and orderly recorder, announced the discovery of *Hippophae rhamnoides* on the Wexford coast and made the following comment:

> "From what I have seen I think there is no doubt that the plant is truly indigenous . . . It may be objected that the sandhills adjoin a large park, where much planting has been carried on, and I did notice in one place a young *Acer pseudoplatanus* growing with the *Hippophae*, and also a plant of *Clematis vitalba*, both evidently self-sown, but there is no appearance of the *Hippophae* itself having been planted, and it is too widely spread to be considered an escape or the remains of former cultivation . . . Miss Farmer has also ascertained that the plant has long been known to the inhabitants, who always believed it to be truly wild".

Convincing enough, one might think, but two or three months later there appeared on p. 373 a further note by More:

> "From information received through Miss Farmer, I learn that the sea buckthorn was first planted on the sandhills at Kiltennel and Courtown by the father of the present Earl of Courtown, about thirty years ago, and since that time the planting has been continued by the present Earl, few years passing without some additions being made . . . This may serve as a caution against deciding too hastily in favour of any plant being indigenous even when it presents every appearance of being perfectly wild".

It may indeed, though the moral is all too often ignored. It also suggests that information supplied by the local landowner will often be of greater value than that supplied by "the inhabitants".

THE SOLUTION

What, then, is to be our procedure in attempting to decide on status? I suggest that there are eight criteria which may be employed (not all of them applicable to every species), and that although very seldom is any one of them decisive, when several point in the same direction one is justified in accepting the composite evidence as reasonably conclusive. There are, of course, many species for which the evidence will turn out to be very scanty or else conflicting, and in these cases it is best to be honest and to be content with a question-mark as the only answer. The criteria I propose are as follows.

FOSSIL EVIDENCE

A fossil record attributable to a date between the last glaciation and the beginning of neolithic agriculture provides evidence of native status which can be regarded as conclusive. Absence of fossils from this period and plentiful representation at earlier or later dates suggests alien status but cannot prove it. Godwin (1975) provided such evidence of native status for a large number of species, but most of them are plants which nobody ever supposed to be alien, and the list of weeds and ruderals for which such evidence appears to be provided has to be analysed with some caution. In a few cases the date of the deposit is open to question; in a great many more the identification to species level is admittedly speculative or uncertain; and there are more still for which no uncertainty has been expressed but for which some scepticism is justified. I yield to none in my admiration for the monotonous and patient toil that quaternary botanists endure in picking over piles of compost to find in them the occasional seed or leaf-fragment. But we must recognize that nearly all their macroscopic material is of a kind that the normal taxonomist would reject as totally inadequate for identification, and that their pollen, though usually in better condition, is very often identifiable only to genus, and also, if scanty, is subject to doubts as to long-range transport.

Uncertainty of identification can be exemplified by the annual species of the genus *Polygonum*. I have recently had occasion to examine closely the nuts of many of these and, working with the best fresh material, I have concluded that one can identify with fair certainty the nuts of *P. minus* (by their small size) and of *P. hydropiper* (by their microtuberculate surface). The nuts of *P. mite*, *P. persicaria* and *P. lapathifolium* are, however, so much alike that, although if I were shown a collection of 20 nuts from a number of plants of the same species I might hazard a guess (for there are small differences of average size or shape, though with large overlaps), I should never dare to name a single nut. Yet confident identifications of these species have been made from eroded and sometimes fragmentary nuts in post-glacial deposits, based in many cases on characters which have since been abandoned by taxonomists as unreliable, but which still persist in all but the most recent literature.

Some of Godwin's early results gave clear evidence of the existence in Britain in late-glacial times of a few weedy species which had hitherto been regarded as possibly introduced, and a few more have been added by later workers: *Aethusa cynapium*, *Atriplex patula*, *Solanum nigrum* and *Sonchus oleraceus* may be cited as examples. This important finding was given some well-deserved publicity, but the botanical world in general seems to have got an exaggerated idea of the number of species involved, and the policy which followed, of giving almost every species the benefit of the doubt, was carried much too far. A systematic perusal of the pages of Godwin (1975) has left me much more impressed by the number of weeds and ruderals whose first post-glacial appearance lies in the Bronze Age or later than by the number which have reliable records from the late-glacial or the pre-neolithic part of the post-glacial. But it should in fairness be added that a considerable number of indubitably native species also make their first appearance in Bronze or Iron Age times. This demonstrates how relatively scanty the fossil record still is and the danger of argument from absences.

I do not consider that interglacial fossils give more than very slight evidence in favour of native status. (Once more the name of *Rhododendron ponticum* must be whispered). Godwin implies for some species that, although he does not rule out the possibility of extinction during the last glaciation and subsequent re-introduction by man, he is impressed by the evidence afforded by interglacial fossils that they once grew here in habitats not influenced by man. But this was true, not of present conditions, but of interglacial conditions, when the climate, at least for part of the time, was warmer than it is today, and approximated to the present climate of southern Europe, where many of the disputed species are undoubtedly native. An interglacial fossil, therefore, gives at best a hint as to the possibility of native status, but if this hint is not backed up by a post-glacial and pre-neolithic fossil, or by the occurrence of the species in a natural habitat today, I do not think that it has much weight.

To sum up, then, the fossil record gives us firm evidence for the native status of a few disputed species, but only a few.

HISTORICAL EVIDENCE

We know that *Buddleja davidii* was introduced to England as a supposed novelty in 1896; we know that it is now common in places where the flora was carefully studied and listed a century ago without any mention of it. No more need be said. Such evidence can prove alien status; it can never prove the reverse. Less conclusive, but nevertheless suggestive, is the absence from an early list or Flora of a conspicuous plant of doubtful status. I regard *Muscari neglectum* as alien in Britain, and one of my reasons, though not the only one, is that in Cambridgeshire, where it looks as native as anywhere, it was unknown to Ray, but was first recorded by Henslow in 1828.

As a subheading under this criterion one can mention rate of increase or decline, for if this is very noticeable it provides some presumptive evidence for alien status. Native plants do not, as a rule, behave like *Elodea canadensis* or *Veronica persica* in their spread, or like *Sisymbrium irio* or *Agrostemma githago* in their decline. There are, of course, exceptions: *Epilobium angustifolium* may be cited on the one hand and *Orobanche rapum-genistae* on the other. And there are some aliens like

Inula helenium which persist for centuries without marked increase or decrease. But such exceptions are few, and the rule is of considerable value.

HABITAT

If a plant grows only in man-made habitats it is likely to be alien; if it grows extensively in more or less natural habitats it is likely to be native. This is a sound principle but is, again, subject to qualification and exceptions. Firstly, a few aliens are extensively naturalized in natural habitats; *Epilobium nerterioides* and *Rhododendron ponticum* are perhaps the best examples. On the other hand we must acknowledge the possibility that for some species the natural habitat has virtually disappeared, and that they survive today as refugees in man-made habitats. On the whole, however, it seems fairly safe to regard as alien those species which are very seldom seen except as field or garden weeds, and to admit as native such species as *Anagallis arvensis* and *Stellaria media* which, though commonest as weeds, are seen fairly often in other habitats such as sand-dunes.

This criterion is most useful for weeds; for ruderals it gives less certain guidance, since their habitat is often intermediate between the natural and the artificial, and since plants can arrive in ruderal habitats from very various sources. Hedgerows are particularly difficult to assess from this point of view; they are certainly rich in native woodland plants, but they are also rich in undoubted aliens. For woodland species suspected of alien status, the habitat gives few clues one way or the other, except that one might expect a native to be most abundant in those woods which are furthest from houses and subject to least disturbance, and an alien to be commonest in hedgerows, copses near houses, and woods of large demesnes. By this criterion I think that the snowdrop fails to establish its native status.

GEOGRAPHICAL DISTRIBUTION

This can never give a decisive answer, but it can give a strong hint. For it is reasonable to assert that although striking examples can be found of disjunct but undoubtedly native distributions, more or less continuous distributions are much commoner. If, therefore, a plant of southern England is not accepted as native by the botanists of Holland, Belgium, or France north of Paris, I think that the burden of proof lies on those who wish to treat it as native in England. Sometimes, as with *Arabis stricta* and *Gagea bohemica*, they will be able to put up a good case, but more often not. It is always advisable, when assessing evidence of this type, to consult Hegi's *Illustrierte Flora von Mittel-Europa*, which gives a saner and more careful assessment of the native range of most European plants than any other book I know.

Even among disjunct distributions we can distinguish between those which, improbable though they may appear, are shown by several species, which thereby give each other mutual support for their claim to native status, and others which are unique, and for that reason to be regarded with more suspicion. It is this consideration which helps to justify the claim for native status in Ireland for *Hypericum canadense* made by Webb & Halliday (1973), while no such claim is made for *Juncus planifolius*, which grows not far away in a not very dissimilar habitat. For although there are a few species for which a native bipolar distribution has been claimed, they are all more widely distributed in the northern hemisphere and relatively local in the south; no species is known which is widely distributed in what one may call *Nothofagus*-land and confined to one or two native localities in the north temperate zone. If *Juncus planifolius* were native in Ireland it would represent a unique pattern of distribution, and this fact, coupled with the knowledge that it is naturalized also in Hawaii, is enough to outweigh the difficulty of accounting for the transport of its seeds to a Connemara bog by any known human agency. But there are several species other than *Hypericum canadense* common to north-eastern North America and north-western Europe, and to accept it as native in Ireland raises no problem that is not already raised by *Eriocaulon aquaticum* and *Spiranthes romanzoffiana*.

FREQUENCY OF KNOWN NATURALIZATION

If a plant claimed to be native in one locality is becoming more and more widely naturalized in similar habitats not far away, then some reconsideration is called for. Such naturalization cannot prove that it is not native in the first station, but it constitutes strong circumstantial evidence against the claim. *Lonicera xylosteum* provides a good example. It has long been accepted as native in one station near Arundel; this can be traced back to a statement by Borrer, published by Smith (1801), that here it was "growing plentifully and certainly wild". But Borrer was only 19 at the time; the plant still grows in or near his station, but not plentifully; Smith admitted at the time that it was frequent in gardens and that he had previously regarded it as an escape; and Perring & Walters (1962) show just one hundred stations in England and Wales where it is held to be probably or certainly naturalized. I cannot believe that the statement by the youthful Borrer, copied uncritically from one book to another, outweighs the mass of evidence in the opposite direction.

GENETIC DIVERSITY

It seems reasonable to suppose that if the weed populations of a species show obvious genetic differences from small populations found in natural habitats it is more likely to be native than if the two populations are more or less identical. This is because the pressures on a plant of open ground to adapt itself for life as a weed are greater than are those on an escaped weed to adapt itself to a natural open habitat. The observations by Akeroyd *et al.* (1978) on *Senecio viscosus* seem for this reason to give a little support to the supposition that it is native on shingle beaches, though they would need to be considerably extended before they could be regarded as really compelling. Unfortunately there are very few species for which the relevant data are available.

REPRODUCTIVE PATTERN

It seems reasonable to assume that most native plants are capable of reproducing, at least in part, by seed, and that if a plant reproduces entirely vegetatively it can legitimately be suspected of being an alien. There are, of course, some exceptions to the first part of this statement; they are mostly polyploids of arctic-alpine affinities (*Polygonum viviparum*, *Festuca vivipara*), plants of extremely local relict distribution (*Erica mackaiana*, *Saxifraga cernua*), or self-sterile species with large local clones, such as *Lysimachia nummularia*. The statement is not, of course, convertible, as many aliens reproduce entirely by seed. But even if one did not know from other evidence that it is alien, the sterility of *Veronica filiformis* would bring it under suspicion, and I find it hard to believe that *Petasites hybridus* is native in those rather extensive districts where plants of only one sex are to be found.

POSSIBLE MEANS OF INTRODUCTION

If a species is to be confidently classed as an alien it is obviously desirable that one should have some idea about how it came to be introduced. If no such mechanism can be suggested it is an argument in favour of native status, though this may be overruled by other considerations, as we have seen in the case of *Juncus planifolius*. The various arguments must be weighed against each other as fairly as possible, and the conclusion adopted which, even if rather improbable, seems less improbable than the alternatives.

Who is best qualified to do this weighing? It is hard to say. Detailed local knowledge is often invaluable, but all too often its value is eroded by local patriotism. There is a curious emotional bias, which I have found very widespread (and from which I may not be entirely free myself), which favours native status for an attractive plant or for the botanist's home county. For this reason a cool assessment by an outsider may be more reliable.

SPECIES REQUIRING RECONSIDERATION

It will have become clear to the reader that the scepticism expressed in this paper is somewhat unilateral, for I believe that far more aliens are represented as native than *vice versa*. I conclude, therefore, by presenting a list of species which are accepted as native without question by Clapham *et al.* (1962), but which are in my opinion probably, and in some cases almost certainly, introduced by man. The list is not intended as exhaustive; I have confined it to what seem to be the clearest cases. The order of species follows Tutin *et al.* (1964–80).

Urtica urens
Polygonum rurivagum
Bilderdykia (Fallopia) convolvulus
Ranunculus sardous
Fumaria officinalis
F. parviflora
Lepidium ruderale
Coronopus squamatus
Reseda luteola
R. lutea
Euphorbia exigua
E. peplus
Lavatera cretica
Eryngium campestre
Scandix pecten-veneris
Torilis nodosa
Lithospermum arvense
Echium plantagineum
Anchusa arvensis
Lamium purpureum
L. amplexicaule
Stachys arvensis
Misopates orontium
Kickxia elatine
K. spuria
Veronica triphyllos
V. polita
V. agrestis
Melampyrum arvense
Orobanche minor
Lonicera xylosteum
Valerianella rimosa
Legousia hybrida
Anthemis arvensis
A. cotula
Chamomilla recutita
Centaurea cyanus
Muscari neglectum
Poa annua
Bromus sterilis
Cynodon dactylon

REFERENCES

Akeroyd, J. R., Warwick, S. I. & Briggs, D. (1978). Variation in four populations of *Senecio viscosus* L. as revealed by a cultivation experiment. *New Phytol.*, **81**: 391–400.

Clapham, A. R., Tutin, T. G. & Warburg, E. F. (1962). *Flora of the British Isles*, 2nd ed. Cambridge.

Godwin, H. (1975). *The history of the British flora*, 2nd ed. Cambridge.

Healy, A. J. & Edgar, E. (1980). *Flora of New Zealand*, **3**: ix. Wellington.

Martin, W. K. & Fraser, G. T. (1939). *Flora of Devon*, pp. 348–349. Arbroath.

More, A. G. (1868a). *Hippophae rhamnoides* in Ireland. *J. Bot., Lond.*, **6**: 255–256.

More, A. G. (1868b). *Hippohae rhamnoides* not indigenous in Ireland. *J. Bot., Lond*, **6**: 373.

Perring, F. H. & Walters, S. M., eds (1962). *Atlas of the British flora.* London.

Smith, J. E. (1801). *Lonicera xylosteum*, in Sowerby, J. *English botany*, **13**: plate 916. London.

Tutin, T. G. (1962). *Eryngium*, in Clapham, A. R., Tutin, T. G. & Warburg, E. F. *Flora of the British Isles*, 2nd ed., pp. 502–503. Cambridge.

Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M. & Webb, D. A., eds (1964–1980). *Flora Europaea*, **1–5**. Cambridge.

Webb, D. A. & Halliday, G. (1973). The distribution, habitat and status of *Hypericum canadense* L. in Ireland. *Watsonia*, **9**: 333–344.

(*Accepted May 1984*)

Watsonia, **15**, 237–252 (1985)

Bird seed aliens in Britain

C. G. HANSON

1 Coltsfoot Road, Ware, Herts., SG12 7NW

and

J. L. MASON

Nature Conservancy Council, Attingham Park, Shrewsbury, SY4 4TW

ABSTRACT

The petfood industry imports large quantities of seed into Britain as food for cage birds. This ultimately results in the appearance of many species of plants growing in Britain as casuals on rubbish tips or waste ground and in gardens. Some 30 species of plants are regularly introduced as bird food and these, together with their impurities, regularly appear as bird seed aliens. These plants originate widely from many countries around the world. Cultivation of bird seed samples from many sources and the records of plants occurring as bird seed aliens have produced a list of 438 species of plants believed to be introduced by this agency.

INTRODUCTION

Alien plants may be introduced deliberately or accidentally into Britain by the activities of man. Lousley (1953) listed agencies by which foreign cultivated plants and weeds may be introduced into this country. He pointed out that it is useful to distinguish (a) those plants which are brought in deliberately and (b) those which come in accidentally. In the category (b) are a number of groups of alien weeds that have received a good deal of attention from botanists in the past. Wool aliens, for example, were studied by Hayward & Druce (1919) and Lousley (1961) and many others. Dock aliens introduced with ballast were studied by Sandwith (1933) and others.

The import of foreign seed as foodstuffs for domestic and cage birds is a major source of introduction of aliens which has received little attention or detailed study. A large proportion of the foreign plants that appear as casuals on town rubbish tips every summer originate from bird cage waste in domestic rubbish. There are a number of other situations in which bird seed plants may appear as casuals. Mixtures sold as wild bird food are often scattered in gardens or on waste ground where some of the seeds germinate. There are also rare instances where waste from importers of grain is dumped or spilled on waste land where some of the seeds may grow.

Müller (1950) listed plants introduced into Germany with bird seed in the only comprehensive paper on the subject to date. Hovda (1978) published a list of plants cultivated from bird seed in Oslo. There are a number of more popular accounts in the British literature that will be of interest to students of bird seed aliens. McClintock (1967, 1972) gave short accounts of the more familiar bird seed plants. Mason (1971) described species introduced into gardens with bird food mixtures. Mason (1973–76) gave guidance on the identification of some of the most frequent bird seed aliens in a series of illustrated articles. Watts & Watts (1979) made a painstaking analysis of the composition of commercial bird seed mixtures and related it to the occurrence of weeds on a Norwich rubbish tip.

The present paper attempts to give a brief account of the bird seed industry and the part it plays in bringing alien plants into this country. It also presents the results of the authors' work on cultivating plants from commercial bird food mixtures, in the form of a definitive list of species that may be introduced into Britain by this agency.

BIRD FOOD PLANTS

There are about 30 different plants whose seed is imported into Britain as bird food. The seed is fed to a variety of different types of domestic and cage birds such as chickens, pigeons, parrots, budgerigars and canaries. Mixtures of commercial seed for these birds vary from one producer to another but the basic ingredients are usually the same. Many of the plants imported as seed in this way are grown in warmer countries for local consumption. Only a small proportion of the total production is used as bird food. Some of the plants yield a variety of products, such as Hemp, *Cannabis sativa*, which is grown to produce fibre and narcotic resin in addition to the seeds. Few of the plants are grown purely as bird food but Canary Grass, *Phalaris canariensis*, is a good example of a plant which is rarely grown for human consumption and is primarily produced as a bird food.

Cereal grasses account for the majority of bird foods and are currently imported in tens of thousands of tonnes per annum. *P. canariensis* and the various millets (species of *Panicum*, *Setaria* and *Echinochloa*) are the principal imports. *P. canariensis* is imported from a number of producing countries among which Morocco and Argentina are the most important. It is also grown in Greece, Turkey, Spain, Australia, Canada, the U.S.A., Holland and England. Yields in this country are low compared with cash crops such as Barley so it is hardly grown here commercially. Millets include the seeds of several different species of plant that are sold under trade names which give little clue about the nature of the actual plant in some cases. Broomcorn Millet, *Panicum miliaceum*, is widely grown as a food crop for man and his livestock, especially in Asia. A number of colour varieties are imported from America such as 'Red Dakota' and 'White Colorado' from the U.S.A. and 'Plate Yellow' from Argentina. Italian or Foxtail Millet, *Setaria italica*, is widely grown and commonly used for human food, but also for fodder and for brewing beer. This plant is sold as intact ears in the form of millet sprays for budgerigars and is imported from Italy, France and China in this form. The loose grain is sold under the misleading trade name 'Panicum Millet' and is imported from the U.S.A., S. Africa, Australia, China and France. A proportion of the millet imported is Japanese Millet, *Echinochloa utilis*, which originates from Australia, S. Africa and the U.S.A.

Rice, *Oryza sativa*, is also used as a bird food under the name 'Paddy Rice' and is imported from Italy and Argentina. Other less exotic cereals of temperate countries such as Maize, *Zea mays*, Barley, *Hordeum distichon* and *H. vulgare*, Wheat, *Triticum aestivum*, and possibly Rye, *Secale cereale*, are also used in bird foods. A number of other species are also imported as bird foods, especially members of the Compositae. Sunflower, *Helianthus annuus*, which is used for parrots, is imported from the East African countries Kenya, Uganda and Tanzania. Another composite, *Guizotia abyssinica*, yields the black seeds of Niger which are imported from Ethiopia and India. The large thistle-like Safflower, *Carthamus tinctorius*, produces oily seeds that are introduced from India, the U.S.A. and Australia. *Cannabis sativa* is another plant of warmer climates which produces useful oily seeds. This is another common ingredient of bird food mixtures and is imported from such countries as Turkey and China.

A number of plants grown in Europe are imported as bird food, including Teazel, *Dipsacus sativus*, (which is soaked and used for rearing young birds); Gold of Pleasure, *Camelina sativa*; Buckwheat, *Fagopyrum esculentum*; 'Linseed', *Linum usitatissimum*, from Holland; the aromatic umbellifer Cumin, *Cuminum cyminum* (a tonic seed), from Cyprus and elsewhere; and Sweet Pepper, *Capsicum annuum*, from Spain.

From this brief review it will be clear that bird food is imported from a wide variety of sources and that only a small proportion of the production of these plants is exported to Britain as bird food. The actual sources of seed may vary from one year to the next depending on the success of the harvest in the producing countries and how this influences the price on the world market. Other factors such as local needs may also have some bearing on the amount exported by certain countries.

Most of the really frequent bird seed aliens belong to this group of intentionally imported plants. In the list which follows this account, the common commercial names of seeds used as bird food are given together with their appropriate scientific names. The majority of these plants will grow readily in Britain and frequently appear as casuals on waste ground, rubbish tips, etc. A few of them virtually never appear here because they are imported in very small quantity or they have little chance of finding suitable conditions for germination. For example Groundnut, *Arachis hypogaea*, and *Cuminum cyminum* are rare as casual plants, while the authors have never seen *Oryza sativa* growing wild in Britain.

THE BIRD FOOD INDUSTRY

The processes involved in the preparation of commercial bird seed were described by Byles (1968), who gave some background information about the bird food industry. The various seeds first arrive in this country from foreign sources in sacks which contain a large proportion of unwanted material such as husks, stalks, straw, soil, stones, fragments of insects, pieces of newspaper and other rubbish. The imported seed also includes foreign seeds of the weeds which were harvested with the crop. The condition of seed on arrival depends on the type of crop and the country of origin. *Phalaris canariensis* seed arriving from Morocco, for example, is spectacularly impure with a great quantity of foreign seed. The seed is cleaned first by sieving to remove stones, soil and some foreign matter, and by blowing to remove dust and chaff. The seed is then sorted using a revolving drum which is lined with indentations the size and shape of the desired seed. The drum picks up only seeds of the appropriate dimensions. This results in a fairly pure seed supply which is then polished clean. The few foreign seeds that escape the cleaning process are those that resemble the main seed most closely in size and shape. If commercial packets of budgerigar seed are carefully sorted they reveal a few foreign seeds of plants such as *Lolium temulentum*, *Setaria pumila*, *Hainardia cylindrica* and *Centaurea diluta*, which closely resemble *Phalaris canariensis* seeds in size.

There are a number of dealers in the U.K. who sell seed as bird food either as pure seed or in a variety of proprietary mixtures such as 'Budgie Mixture', 'Canary Mixture' or 'Parrot Food'. This seed may be very clean and pure or it may contain a fair proportion of foreign matter which has not been adequately removed during the cleaning process. Some mixtures include tonic and other additives to give a balanced diet. Mixtures for garden birds are often produced under the name 'Wild Bird Food': the best known of these is 'Swoop'. These mixtures often consist of some staple food seeds together with a proportion of the cleanings from other commercial seed mixtures. These cleanings include a great variety of weed seeds which are imported as impurities. This is why such bird seed often introduces exotic plants into people's gardens.

The high quality cage bird mixtures are carefully finished products which are intended to look attractive to the buyer. These include Petfoods' 'Trill' and Capern's 'Canary Mixture'. The seed is very pure, with few foreign seeds; the seed types in such a mixture often include colour varieties to improve the appearance and all the grains are free of dust and debris as a result of being polished clean.

FACTORS INFLUENCING ALIENS APPEARING IN BRITAIN

There are a number of factors which influence the bird seed alien plants that may appear growing wild as casuals in Britain. Most of the bird food species themselves are introduced in quantity but, for reasons already discussed, not all of them occur as casual plants. The great variety of other bird seed aliens are provided by the foreign material which is inevitably imported with the bird food itself. Certain products are imported in a more impure state than others. The opportunity to introduce foreign seeds varies with the type of plant, how it is harvested and which country it comes from. Some species can be harvested easily without gathering much foreign material, e.g. *Dipsacus sativus*, *Zea mays* and *Helianthus annuus*, while the low-growing cereals such as the millets cannot be easily separated from the weeds that grow with them. The country of origin of the seed clearly influences the actual species that may be introduced with it. Consequently changes in the main sources of different types of seed in response to a fluctuating world market can result in changes in the aliens commonly occurring in Britain. This probably explains why some weeds make regular appearances for a period of years and then are absent for a number of years.

Certain species pass through the cleaning process more easily than others. There are a number of species whose seeds are introduced into this country in large quantities as impurities, but which are very easily separated from the bird food and which therefore rarely have the opportunity to germinate. These include the very large fruits of plants such as *Scandix pecten-veneris*, *Tragopogon hybridus*, *Xanthium spinosum* and *Cenchrus incertus*. The tiny seeds of species of *Chenopodium* and *Amaranthus* are also relatively easily removed. As explained above, the most regular weeds are those whose seeds closely resemble the main bird food plants.

CULTIVATION OF BIRD SEED

It is difficult to produce a definitive list of bird seed aliens by compiling a list of plants recorded as casuals on rubbish tips and waste ground because the plants that occur in such places may be introduced with a variety of other products in addition to bird seed. A number of the frequent bird seed aliens are widespread or cosmopolitan weeds that are also introduced into Britain with wool, esparto grass and soya beans. In order to eliminate the element of doubt about the origin of weeds the authors carried out a programme of cultivating samples of bird seed in gardens and greenhouses under controlled conditions using sterilized soil. The samples included commercial bird seed mixtures and the cleanings from a variety of different sources that were obtained from the bird seed distributors. Pigeon and chicken foods were excluded.

ANNOTATED LIST OF SPECIES INTRODUCED INTO BRITAIN WITH BIRD FOOD

The following list is based on the cultivation of samples of bird seed and the waste separated from commercial seed carried out by the authors with some additional records contributed by those listed below. The list also includes species recorded on the waste tips between Humberstone and Cleethorpes in N. Lincs., v.c. 54 (now S. Humberside), that received waste from a large petfood distributor. Records are also included from other tips, where there was little doubt that the plants originated from bird seed, and from gardens where bird seed had been distributed. The species imported and sold as bird food are distinguished by the use of block capitals. The remainder are imported as impurities in the main staple crops. The following abbreviations are used in the list:

Cult. = cultivated by:
CGH = C. G. Hanson
JLM = J. L. Mason
FH = Mrs F. Houseman
CJJ = C. J. Jenness
DNT = D. N. Turner
GDW = Dr G. D. Watts
Müller = recorded in Müller's list (Müller 1950)
Hovda = recorded in Hovda's list (Hovda 1978)
Lincs. 1956, etc. = recorded on tips between Humberstone and Cleethorpes (Gibbons 1975)
tips = recorded on other rubbish tips with bird seed aliens*
gardens = recorded in gardens in association with other bird seed aliens*

very frequent	= seen every year in quantity	authors' assessment of frequency in the wild as casuals of tips, waste ground, etc., with advice from E. J. Clement
frequent	= seen every year	
infrequent	= a few plants seen every year	
occasional	= a few plants seen most years	
sporadic	= single plants appearing irregularly	

The nomenclature and sequence of families follow *Flora Europaea*. The genera and species are listed in alphabetical order within families.

Cannabaceae

CANNABIS SATIVA L. (INDIAN HEMP): Cult. CGH & JLM; Müller; Hovda; Lincs. 1956; tips; frequent. A regular ingredient of bird seed mixtures which is often sold as sterile seed to prevent misuse of the plant as a narcotic drug.

Polygonaceae

Bilderdykia convolvulus (L.) Dumort. (*Polygonum convolvulus* L.): Cult. CGH & JLM; Müller; frequent.

Emex spinosa (L.) Campd.: Cult. CGH & JLM. The seeds are a regular impurity in imported seed but the plant itself is a rare weed.

FAGOPYRUM ESCULENTUM Moench (BUCKWHEAT): Cult. CGH; Müller; Lincs. 1969; tips; frequent. Also used for game rearing.

---

*held in CGH card index

F. tataricum (L.) Gaertner: tips; gardens; sporadic.
Polygonum arenarium subsp. *pulchellum* (Loisel.) D. A. Webb & Chater: Lincs. 1955; tips; sporadic.
P. aviculare L.: Cult. CGH & JLM; Lincs. 1956; very frequent.
P. lapathifolium L.: Cult. CGH; Müller; Lincs. 1956; frequent.
P. nepalense Meissner: Cult. CGH; gardens; sporadic.
P. patulum Bieb.: Müller; Lincs. 1955; tips; sporadic.
P. persicaria L.: Cult. CGH; occasional.
Rumex acetosella L.: Cult. CGH; tips; occasional.
R. brownii Campd.: Cult. CGH. Also not uncommon as a wool alien.
R. crispus L.: Cult. CGH; Müller; infrequent.
R. obovatus Danser: Cult. CGH; tips; gardens; sporadic.
R. pulcher L. subsp. *divaricatus* (L.) Murb.: Cult. CGH; Müller; tips; sporadic.
R. pulcher subsp. *pulcher*: Cult. CGH.
R. triangulivalvis (Danser) Rech.f.: Cult. FH; tips; sporadic.

Chenopodiaceae

Atriplex hortensis L.: Cult. CGH; tips; frequent. Also a garden escape.
A. patula L.: Cult. CGH. Also occurs as a common weed.
Beta vulgaris L.: Cult. CGH; Müller. Also occurs as a garden throw-out.
Chenopodium album L.: Cult. CGH & JLM; Müller; very frequent.
C. album subsp. *striatum* (Krašan) J. Murr: Cult. CGH.
C. ambrosioides L.: tips; sporadic.
C. capitatum (L.) Asch.: Cult. FH; tips; sporadic.
C. ficifolium Sm.: Cult. CGH & JLM; Lincs. 1965; tips; frequent.
C. giganteum D. Don: Cult. CGH; Lincs. 1963; tips; gardens; occasional.
C. glaucum L.: Hovda; tips; sporadic.
C. hybridum L.: Cult. CGH; tips; gardens; infrequent.
C. murale L.: Cult. CGH; Lincs. 1953; infrequent.
C. opulifolium Schrader ex Koch & Ziz: Cult. CGH; Müller; Lincs. 1955; occasional.
C. polyspermum L.: Cult. CGH; Hovda; very frequent.
C. probstii Aellen: Cult. CGH & JLM; frequent.
C. rubrum L.: Cult. CGH; very frequent.
C. suecicum J. Murr: Cult. CGH; Hovda.
C. vulvaria L.: Cult. FH; tips; gardens; sporadic.
Salsola kali subsp. *ruthenica* (Iljin) Soó: tips; gardens; sporadic.
Spinacia oleracea L.: Cult. CGH; Müller; tips; occasional.

Amaranthaceae

Achyranthes aspera L.: Cult. CGH; tips; sporadic.
Amaranthus × *adulterinus* Thell.: Cult. CGH; tips; sporadic.
A. albus L.: Cult. CGH & JLM; Müller; Hovda; tips; infrequent. Sometimes becomes temporarily established on rubbish tips and waste ground.
A. blitoides S. Watson: Cult. CGH; Lincs. 1955; occasional. A characteristic impurity of seed from the Americas.
A. bouchonii Thell.: tips; sporadic.
A. caudatus L.: Cult. CGH; Müller; tips; occasional.
A. cruentus L.: Cult. CGH; sporadic.
A. cruentus var. *erythrostachys* Moq.: Cult. CGH.
A. graecizans L.: Cult. CGH; gardens; sporadic.
A. hypochondriacus L. (*A. hybridus* L.): Cult. CGH & JLM; infrequent. Common as an impurity in seed imported from the Americas but not so common as a weed.
A. lividus L.: Cult. CJJ; tips; sporadic.
A. muricatus (Moq.) Gillies ex Hicken: tips; gardens; sporadic.
A. paniculatus L.: Müller; gardens; sporadic.

A. quitensis Kunth: Cult. CGH; Müller; tips; infrequent. A common impurity in seed imported from the Americas.
A. retroflexus L.: cult. CGH & JLM; Müller; Hovda; Lincs. 1969; infrequent but the seeds are commonly imported from the Americas.
A. scleropoides Uline & Bray: Cult. CGH & CJJ. An endemic of Texas.
A. standleyanus Parodi ex Covas: Cult. CGH; tips; gardens; sporadic.
A. thunbergii Moq.: tips; sporadic.
A. viridis L.: Cult. CJJ; tips; sporadic.
Celosia argentea L.: Cult. CGH.

Tetragoniaceae
Tetragonia tetragonoides (Pallas) Kuntze: Cult. CGH; tips; occasional.

Portulacaceae
Portulaca oleracea L.: Cult. CGH; Müller; tips; gardens; sporadic.

Caryophyllaceae
Agrostemma githago L.: Müller; gardens; sporadic. Not uncommon near poultry runs.
Silene alba (Miller) E. H. Krause: Cult. CGH.
S. behen L.: Cult. CGH; tips; gardens; sporadic.
S. dichotoma Ehrh.: Cult. CGH & JLM; Müller; gardens; sporadic.
S. gallica L.: Cult. CGH; Lincs. 1955; sporadic.
S. inaperta L.: Cult. CGH; Lincs. 1964; tips; sporadic.
S. laeta (Aiton) Godron: Cult. CGH.
S. muscipula L.: Müller; Lincs. 1963; sporadic.
S. noctiflora L.: Cult. CGH; Müller; occasional.
S. nocturna L.: Cult. CGH.
S. nutans L.: gardens; sporadic.
S. sedoides Poiret: Lincs. 1955; sporadic.
S. vulgaris (Moench) Garcke: Cult. CGH; Müller; frequent but probably usually occurs as a native weed.
S. vulgaris subsp. *angustifolia* (Miller) Hayek: Cult. CGH.
Stellaria media (L.) Vill.: Cult. CGH. Also occurs as a common weed.
Vaccaria pyramidata Medicus: Cult. CGH & JLM; Müller; Hovda; Lincs. 1956; infrequent. A regular impurity in Moroccan seed; often attracts attention because of its decorative flowers.

Ranunculaceae
Nigella gallica Jordan: gardens; sporadic.
Ranunculus arvensis L.: Cult. CGH; Müller.
R. marginatus D'Urv.: Cult. CGH; Lincs. 1956; sporadic.
R. muricatus L.: Cult. CGH; Lincs. 1956; sporadic.

Papaveraceae
Argemone mexicana L.: Cult. CGH; tips; sporadic.
Glaucium corniculatum (L.) J. H. Rudolph: Cult. FH.
[*Papaver atlanticum* (Ball.) Cosson: is claimed to be a bird seed alien in Clapham *et al.* (1962) but the authors have no evidence of its introduction in this way].
P. rhoeas L.: Cult. CGH; Müller; very frequent.
P. SOMNIFERUM L. (BLUE MAW SEED): Cult. CGH & JLM; Müller; Hovda; Lincs. 1956; very frequent. A regular weed also originating from gardens.
P. somniferum L. subsp. *setigerum* (DC.) Corb.: Cult. CGH: Müller; Hovda; Lincs. 1956; sporadic.

Cruciferae
Barbarea vulgaris R. Br.: Cult. CGH; occasional.
Brassica carinata A. Br.: Cult. CGH; occasional.
B. juncea (L.) Czern.: Cult. CGH; Hovda; Lincs. 1956; infrequent, but easily overlooked.

B. napus L.: Cult. CGH; Hovda; frequent.
B. nigra (L.) Koch: Cult. CGH; Hovda; frequent.
B. oleracea L.: Cult. CGH & JLM; infrequent.
B. RAPA L. (RED & BLACK RAPE): Cult. CGH & JLM; Müller; Hovda; frequent. The seed is sold in two colour varieties.
Bunias orientalis L.: Cult. CGH; occasional.
Camelina microcarpa Andrz. ex DC.: is often quoted as a bird seed alien but has not yet been recorded by the authors.
C. SATIVA (L.) Crantz (GOLD OF PLEASURE): Cult. CGH & JLM; Müller; Lincs. 1953; infrequent but sometimes abundant on tips.
Capsella bursa-pastoris (L.) Medicus: Cult. CGH; very frequent.
Conringia orientalis (L.) Dumort.: Cult. CGH; Müller; occasional.
Diplotaxis muralis (L.) DC.: Cult. FH; Hovda; Lincs. 1956; infrequent.
Eruca vesicaria (L.) Cav. (*E. sativa* Mill.): Cult. CGH & JLM; Müller; occasional. Also cultivated and used as a herb or salad plant.
Erucastrum gallicum (Willd.) O. E. Schulz: Cult. CGH; Hovda; sporadic.
Erysimum cheiranthoides L.: Cult. CGH.
Hirschfeldia incana (L.) Lagrèze-Fossat: Cult. CGH; frequent and may become established on waste ground.
Lepidium bonariense L.: gardens; sporadic.
L. densiflorum Schrader: gardens; sporadic.
L. divaricatum Solander: Cult. FH.
L. ruderale L.: Cult. CGH; Lincs. 1963; tips; occasional.
L. sativum L.: Cult. CGH & JLM; Lincs. 1955; frequent.
Lobularia maritima (L.) Desv.: Lincs. 1955; infrequent.
Myagrum perfoliatum L.: Müller; Lincs. 1956; sporadic.
Neslia paniculata (L.) Desv.: Cult. FH & DNT; Müller; Lincs. 1956; sporadic. Often quoted as a bird seed alien but rarely seen.
Raphanus raphanistrum L.: Cult. CGH; Müller; Hovda; occasional.
R. sativus L.: Cult. CGH & JLM; Müller; Lincs. 1963; frequent. A common impurity in Argentinian bird seed. Also cultivated.
Rapistrum perenne (L.) All.: Lincs. 1955; sporadic.
R. rugosum (L.) All.: Cult. CGH & JLM; Müller; Hovda; Lincs. 1963; infrequent.
R. rugosum subsp. *linnaeanum* Rouy & Fouc. (*R. hispanicum* (L.) Crantz): Cult. CGH & JLM.
R. rugosum subsp. *orientale* (L.) Arcangeli (*R. orientale* (L.) Crantz): Cult. CGH; Müller.
Rorippa islandica (Oeder) Borbàs: Cult. CGH; tips; infrequent.
R. sylvestris (L.) Besser: Cult. CGH; sporadic.
Sinapis alba L.: Cult. CGH & JLM; Müller; Hovda; Lincs. 1956; tips; very frequent, but probably overlooked as a bird seed alien.
S. arvensis L.: Cult. CGH; Müller; Hovda; frequent but alien plants probably overlooked.
Sisymbrium altissimum L.: Cult. FH; Lincs. 1956; frequent.
S. orientale L.: Cult. CGH; Hovda; Lincs. 1956; frequent but alien occurrences probably overlooked.
Thlaspi arvense L.: Cult. CGH; frequent.

Resedaceae

Caylusea abyssinica (Fres.) Fisch. & Mey.: Cult. CGH; Müller.
Reseda alba L.: tips; sporadic.

Rosaceae

Potentilla norvegica L.: Cult. CGH. Also recorded from chicken runs.

Leguminosae

ARACHIS HYPOGAEA L. (MONKEY NUT, GROUND NUT or PEANUT): Cult. CGH; tips; sporadic.

CICER ARIETINUM L. (CHICKPEA): Cult. CGH & JLM; tips; occasional. Also has a culinary use in Greek and eastern food.

Coronilla scorpioides (L.) Koch: Cult. CGH & JLM; Müller; tips; gardens; sporadic.

Glycine max (L.) Merr.: Cult. CGH; Müller; tips; gardens; occasional.

Lathyrus annuus L.: gardens; occasional.

L. aphaca L.: Cult. CGH; Müller; Lincs. 1956; infrequent.

L. articulatus L.: Cult. CGH; Müller; gardens; infrequent.

L. cicera L.: Cult. CGH & JLM; Müller.

L. hirsutus L.: Müller; tips; gardens; sporadic.

L. latifolius L.: Cult. CGH. Cultivated in gardens for its garish flowers.

L. sativus L.: Cult. CGH; tips; occasional.

Lens culinaris Medicus: Cult. CGH & JLM; Müller; tips; infrequent. Also introduced for culinary use.

Medicago ciliaris (L.) All.: Cult. CGH.

M. intertexta (L.) Miller: gardens; sporadic.

M. lupulina L.: Cult. CGH; Müller; occasional.

M. polymorpha L. (*M. hispida* Gaertner): Cult. FH; Müller; Lincs. 1955; sporadic. Also very common in wool waste.

M. sativa L.: Cult. CGH; Hovda; frequent. Commonly persists after cultivation as a fodder crop.

M. sativa subsp. *falcata* (L.) Arcangeli: Cult. FH.

Melilotus alba Medicus: Cult. CGH; Lincs. 1956; occasional.

M. indica (L.) All.: Cult. CGH; Müller; Hovda; Lincs. 1956; infrequent.

M. infesta Guss.: Lincs. 1956; tips; sporadic.

M. messanensis (L.) All.: tips; sporadic.

M. officinalis (L.) Pallas: Cult. CGH; Müller; Lincs. 1955; frequent.

M. sulcata Desf.: Cult. CGH & JLM; Müller; tips; gardens; occasional. Distinctive in fruit but may be overlooked as *M. indica*.

Ononis alopecuroides L.: Cult. DNT.

O. baetica Clemente (*O. salzmanniana* Boiss. & Reuter): Cult. CGH; tips; gardens; occasional.

O. mitissima L.: Cult. CGH; Lincs. 1955; gardens; sporadic.

Phaseolus vulgaris L.: Cult. CGH; Müller; Hovda; frequent.

PISUM SATIVUM L. (MAPLES): Cult. CGH; Müller; tips; infrequent. Sold as pigeon food.

P. sativum subsp. *elatius* (Bieb.) Asch. & Graebner: Cult. CJJ; gardens; sporadic.

P. sativum subsp. *sativum*: Cult. CGH; tips; gardens; occasional.

Psoralea americana L.: Cult. CGH; occasional. An attractive perennial alien which rarely reaches maturity and rarely sets seed in Britain.

P. corylifolia L.: Cult. CGH. One of the few bird seed aliens to originate from India.

Scorpiurus muricatus L.: Cult. CGH & JLM; Lincs. 1964; occasional. The seed is a common impurity in Mediterranean seed but the plant only occasionally appears on tips and gardens as a weed.

S. vermiculatus L.: gardens; sporadic.

Trifolium alexandrinum L.: Lincs. 1956.

T. angustifolium L.: Cult. FH; Müller; gardens; sporadic.

T. echinatum Bieb.: Lincs. 1955; Müller; sporadic.

T. hybridum L.: Cult. CGH; tips; occasional.

T. incarnatum L.: Cult. CGH; tips; sporadic.

T. isthmocarpum Brot.: Cult. CGH.

T. lappaceum L.: Cult. CGH; Lincs. 1955; gardens; sporadic.

T. pratense L.: Cult. CGH; Müller. Common on tips usually as a native.

T. repens L.: Cult. CGH.

T. resupinatum L.: Lincs. 1956; sporadic.

T. resupinatum var. *majus* Boiss. (*T. suaveolens* Willd.): Cult. CGH.

T. scabrum L.: Lincs. 1956.

T. subterraneum L.: Cult. CGH; Müller.

Trigonella caerulea (L.) Ser.: Cult. CGH; Müller; tips; sporadic. Unknown out of cultivation.

T. corniculata (L.) L.: tips; sporadic.

T. foenum-graecum L.: Cult. CGH & JLM; Müller; Lincs. 1956; tips; occasional. Also grown and used as a herb.
T. polyceratia L.: Cult. FH.
Vicia bithynica (L.) L.: Lincs. 1955; tips; sporadic.
V. ervilia (L.) Willd.: Cult. CGH; Müller.
V. FABA L. (TIC BEANS): Cult. CGH; frequent. Also cultivated in gardens and on agricultural land.
V. hirsuta (L.) S. F. Gray: Cult. CJJ; Müller; tips; sporadic.
V. lutea L.: Müller; tips; gardens; sporadic.
V. narbonensis L.: Cult. CGH; Müller; tips; sporadic.
V. pannonica Crantz: Müller; tips; sporadic.
V. SATIVA L. (TARES): Cult. CGH & JLM; Müller; Hovda; infrequent.
V. sativa L. subsp. *nigra* (L.) Ehrh.: Cult. CGH; Müller.
V. tetrasperma (L.) Schreber: Cult. CGH; Müller; tips; infrequent.
V. villosa Roth subsp. *varia* (Host) Corb.: Cult. CGH; Müller; Lincs. 1963; tips; occasional.
V. villosa Roth subsp. *villosa*: tips, sporadic.

Linaceae
Linum bienne Miller: tips; gardens; sporadic.
L. tenue Desf.: gardens; sporadic.
L. USITATISSIMUM L. (LINSEED): Cult. CGH & JLM; Müller; Lincs. 1955; frequent. Also escapes from agricultural cultivation.

Euphorbiaceae
Euphorbia hirta L.: gardens; sporadic.
E. serpens Kunth: Cult. CGH; tips; sporadic.

Malvaceae
Abutilon theophrasti Medicus: Cult. CGH; Müller; tips; infrequent.
Anoda cristata (L.) Schlecht.: Müller; tips; sporadic.
Hibiscus trionum L.: Cult. CGH & JLM; tips; infrequent. An attractive alien which is also cultivated in gardens.
Lavatera trimestris L.: Cult. CGH; gardens; occasional. Also cultivated in gardens.
Malva nicaeensis All.: Cult. CGH; Müller.
M. parviflora L.: Cult. CGH; Müller; Lincs. 1956; occasional.
M. pusilla Sm.: Müller; Lincs. 1956; sporadic.
Sida spinosa L.: Cult. CGH; tips; sporadic. This and other species of *Sida* are also introduced with soya bean waste.

Cucurbitaceae
Sicyos angulatus L.: Cult. CJJ; gardens; sporadic.

Lythraceae
Lythrum junceum Banks & Solander (*L. meonanthum* Link ex Steudel): Cult. CGH; Lincs. 1963; tips; gardens; infrequent.
L. salicaria L.: Cult. CGH. A surprising alien yet cultivated on several occasions.

Umbelliferae
Aethusa cynapium L.: Cult. CGH; tips; very frequent.
Ammi majus L.: Cult. CGH & JLM; Lincs. 1969; tips; gardens; infrequent.
A. visnaga (L.) Lam.: Cult. CGH & JLM; Lincs. 1969; occasional.
Anethum graveolens L.: Cult. CGH, JLM & FH; Lincs. 1964; infrequent. This plant can easily be overlooked as a small fennel, or confused with *Ridolfia* unless in ripe fruit.
Anthriscus caucalis Bieb.: Cult. CGH; tips; occasional.
Bifora testiculata (L.) Roth: Cult. CGH; Müller. Seeds have been seen as an impurity among 'Tares' (*Vicia sativa*).

Bupleurum fontanesii Guss. ex Carvel (*B. odontites* L.): Lincs. 1964; Müller; sporadic.

B. lancifolium Hornem.: Cult. CGH & JLM; Lincs. 1956; gardens; infrequent. A Mediterranean weed whose seeds regularly appear as impurities in commercial bird seed. Often appears as a garden weed and is frequently mis-recorded as *B. rotundifolium* L. which is unlikely to be found in Britain now.

Capnophyllum peregrinum (L.) Lange. (*C. dichotomum*): Cult. CGH & GDW.

CARUM CARVI L. (CARAWAY): Müller; tips; occasional. Also introduced for culinary use.

Caucalis platycarpos L. (*C. daucoides* L.): Cult. CGH & FH; Müller; Lincs. 1956; sporadic.

Coriandrum sativum L.: Cult. CGH & JLM; Lincs. 1963; frequent. Also introduced and grown as a herb.

CUMINUM CYMINUM L. (CUMIN): Cult. CGH; tips; occasional. Also used as a herb or spice.

Daucus carota L.: Cult. CGH; tips; occasional.

D. muricatus (L.) L.: tips; gardens; sporadic.

Hydrocotyle vulgaris L.: Cult. CGH.

Pastinaca sativa L.: Cult. CGH; tips; infrequent.

Petroselinum crispum (Miller) A. W. Hill: Cult. DNT.

PIMPINELLA ANISUM L. (ANISEED): Cult. CGH. Also used for culinary purposes.

Ridolfia segetum Moris: Cult. CGH; Müller; Lincs. 1955; occasional. Easily confused with *Anethum* unless in ripe fruit.

Scandix pecten-veneris L.: Cult. CGH & JLM; Müller; Lincs. 1964; sporadic. The fruits are frequent among seeds imported from the Mediterranean region but the plant itself rarely occurs on tips.

S. stellata Banks & Solander: tips; sporadic.

Torilis arvensis (Hudson) Link subsp. *neglecta* (Schultes) Thell.: Cult. CGH; tips; occasional.

T. leptophylla (L.) Reichenb.: Cult. CGH; Müller; tips; sporadic.

T. nodosa (L.) Gaertner: Cult. CGH & JLM; Müller; Lincs. 1969; gardens; occasional.

Trachyspermum ammi (L.) Sprague ex Turrill: Cult. FH; Lincs. 1969; tips; infrequent. Also introduced as a spice, 'Ajwan'.

Turgenia latifolia (L.) Hoffm. (*Caucalis latifolia* L.): Cult. FH; Müller; gardens; sporadic.

Primulaceae

Anagallis arvensis L.: Cult. CGH; Müller; Lincs. 1956. The plants we have seen have blue flowers with red centres. Genuine *A. foemina* Miller has not been observed as a bird seed weed.

Rubiaceae

Asperula arvensis L.: Cult. CGH & JLM; Müller; Lincs. 1956; gardens; occasional. Introduced from the Mediterranean region. Probably easily overlooked unless in flower.

Crucianella angustifolia L.: Cult. CGH & CJJ; Müller; gardens; sporadic.

Galium aparine L.: Cult. CGH; Müller; very frequent. Introduced plants could be easily overlooked.

G. parisiense L.: Cult. CGH; Müller; gardens; sporadic.

G. tricornutum Dandy: Cult. CGH & JLM; Müller; Lincs. 1956; gardens; occasional. Seeds are regular impurities in imported seed but the plant itself is rarely found.

G. verrucosum Hudson (*G. saccharatum* All.): Cult. CGH; gardens; sporadic.

G. viscosum Vahl (*G. campestre* Schousboe ex Willd.): Cult. CGH.

Convolvulaceae

Convolvulus althaeoides L.: Cult. CGH; tips; gardens; occasional.

C. arvensis L.: Cult. CGH; Müller; infrequent.

C. tricolor L.: Lincs. 1963; tips; gardens; sporadic.

Cuscuta australis R. Br. subsp. *cesattiana* (Bertol.) Feinbrun: tips; sporadic.

C. campestris Yuncker: Cult. CGH; tips; gardens; occasional.

Ipomoea eriocarpa R. Br.: Cult. CGH.

I. hederacea Jacq.: Cult. CGH; tips; gardens; sporadic. This species, both as var. *hederacea* and as the following variety, occurs regularly as a soya bean alien.

I. hederacea var. *integriuscula* Gray: Cult. CGH.

I. purpurea Roth (*Pharbitis purpurea* (Roth) Voight): Cult. CGH; Müller; tips; occasional. Also cultivated as a garden plant.

Boraginaceae

Amsinckia calycina (Moris) Chater: Cult. CGH.

A. intermedia Fisch. & Mey.: Cult. CGH; tips; sporadic.

Anchusa azurea Miller: Cult. CGH & JLM; Müller; occasional. Also cultivated as a decorative garden flower.

Buglossoides arvensis (L.) I. M. Johnstone (*Lithospermum arvense* L.): Cult. CGH & JLM; Müller; Lincs. 1956; occasional.

Cynoglossum lanceolatum Forsk.: Cult. CGH.

Lappula squarrosa (Retz.) Dumort. (*L. myosotis* Moench): Cult. CGH & JLM; Müller; tips; sporadic.

Verbenaceae

Verbena supina L.: tips; sporadic.

Labiatae

Dracocephalum parviflorum Nutt.: tips; sporadic.

Salvia reflexa Hornem.: Cult. CGH & JLM; Lincs. 1953; tips; occasional. Regularly introduced with millet seed from America.

Sideritis romana L.: Cult. CGH.

Teucrium resupinatum Desf.: gardens; sporadic.

Solanaceae

CAPSICUM ANNUUM L. (SPANISH PEPPER): Cult. CGH; tips; occasional.

Datura ferox L.: Cult. CGH; Müller. Occurs more often as a wool alien.

D. stramonium L.: Cult. CGH; Müller; Lincs. 1964; frequent. Persists on some rubbish tips and waste ground.

D. stramonium var. *tatula*: Cult. CGH; tips; occasional.

Hyoscyamus niger L.: Cult. FH; Lincs. 1956. Quite common on tips and waste ground from other sources.

Nicandra physalodes (L.) Gaertner: Cult. CGH & JLM; Lincs. 1963; tips; frequent. Occasionally cultivated in gardens for its attractive flowers and decorative dried fruits.

Physalis peruviana L.: tips; occasional.

P. philadelphica Lam.: tips; sporadic.

Solanum cornutum Lam. (*S. rostratum* Dunal): Cult. CGH; tips; gardens; occasional. A distinctive weed from the U.S.A. where it is the native foodplant of the Colorado Beetle.

S. luteum Miller: tips; sporadic.

S. nigrum L.: Cult. CGH; Lincs. 1963.

S. pseudocapsicum L.: Cult. CGH; tips; occasional.

S. sarrachoides Sendtner: Cult. CGH; sometimes becomes established on waste ground and tips.

S. sisymbrifolium Lam.: tips; sporadic.

Scrophulariaceae

Calceolaria chelidonioides H.B.K.: Cult. FH; gardens; sporadic.

Kickxia elatine (L.) Dumort.: gardens; sporadic.

K. spuria (L.) Dumort.: gardens; sporadic.

Linaria maroccana Hook. f.: tips; sporadic.

Misopates calycinum Rothm.: Cult. CGH; tips; gardens; occasional.

M. orontium (L.) Raf.: Cult. CGH; gardens; infrequent.

Verbascum phoeniceum L.: gardens; sporadic. Also cultivated as an ornamental plant.

Veronica persica Poiret: Cult. CGH; Müller; tips; occasional but often as a native.

V. polita Fries: Cult. CGH.

Pedaliaceae

Sesamum indicum L.: Cult. CGH; tips; occasional.

Plantaginaceae

Plantago afra L. (*P. psyllium* L.): Cult. CGH; Lincs. 1953; occasional. May be mis-recorded as the next species which it closely resembles.

P. arenaria Waldst. & Kit. (*P. indica* L.): Cult. FH; Hovda; tips; gardens.

P. lagopus L.: Cult. CGH; Lincs. 1955; sporadic.

P. lanceolata L.: Cult. CGH; Müller; very frequent. Alien occurrences could be easily overlooked.

P. major L.: Cult. CGH; Müller; very frequent.

Dipsacaceae

Cephalaria syriaca (L.) Roemer & Schultes: Cult. CGH; Müller.

Dipsacus fullonum L.: Cult. CGH; Lincs. 1955.

D. SATIVUS (L.) Honckeny (FRENCH TEAZLE): Cult. CGH; Lincs. 1955; tips; occasional. Also cultivated for finishing cloth.

Compositae

Ambrosia artemisiifolia L.: Cult. CGH; gardens; occasional. Regularly introduced with millet seed from the U.S.A.

Anthemis cotula L.: Müller; Lincs. 1956.

A. ruthenica Bieb.: Lincs. 1956.

A. tinctoria L.: Cult. FH. Also grown as a garden plant.

Arctium minus Bernh.: Cult. CGH. Alien occurrences could easily be overlooked.

Athanasia crithmifolia L.: gardens; sporadic.

Bidens bipinnata L.: Cult. CGH. Not uncommon as a wool alien.

B. biternata (Low) Merr. & Sherff: Cult. CGH.

B. frondosa L. This and the next species occur as casuals on tips but the authors have no certain evidence that they are introduced with bird seed.

B. pilosa L.: Müller.

B. tripartita L.: Cult. CGH; tips; infrequent.

Calendula officinalis L.: Lincs. 1956.

Carduncellus caeruleus (L.) C. Presl (*Carthamus caeruleus* L.): Cult. CGH.

Carduus pycnocephalus L.: Cult. CGH.

C. tenuiflorus Curtis: Cult. CGH & JLM; Müller.

Carthamus lanatus L.: Cult. FH; sporadic. Usually a wool alien.

C. TINCTORIUS L. (SAFFLOWER): Cult. CGH & JLM; Müller; Lincs. 1955; tips; frequent. The seeds are used as a bird food because of their high oil content.

Centaurea calcitrapa L.: Cult. FH; Lincs. 1953; tips; sporadic.

C. cineraria L.: Cult. FH.

C. cyanus L.: Cult. CGH & JLM; Müller; Lincs. 1956; sporadic.

C. diffusa Lam.: Müller; tips; sporadic.

C. diluta Aiton: Cult. CGH & JLM; Lincs. 1964; tips; frequent. Regularly introduced with Canary Grass seed from N. Africa. It can survive mild winters in Britain and is regularly seen on the old parts of rubbish tips.

C. eriophora L.: Cult. CGH.

C. hyalolepis Boiss. (*C. pallescens* Del.): Lincs. 1964; sporadic.

C. melitensis L.: Cult. CGH & JLM; Müller; Lincs. 1953; sporadic.

C. nigra L.: Cult. CGH. Also occurs as a native.

C. solstitialis L.: Cult. CGH; Müller; Lincs. 1953; tips; gardens; occasional. A distinctive weed from the Mediterranean region.

C. solstitialis subsp. *adamii* (Willd.) Nyman: Lincs. 1964; sporadic. A variant that lacks the conspicuous involucral bracts of the type.

C. triumfetti All.: Cult. CGH.

Chamaemelum mixtum (L.) All. (*Anthemis mixta* L.): Lincs. 1964; gardens; sporadic.

Chamomilla suaveolens (Pursh) Rydb. (*Matricaria matricarioides* (Less.) Porter, pro parte): Cult. CGH.

Chrysanthemum carinatum Schousboe: Lincs. 1956.

C. coronarium L.: Cult. CGH & CJ; Lincs. 1953.

C. segetum L.: Lincs. 1956.

Cichorium endivia L.: Lincs. 1956; tips; sporadic.

C. INTYBUS L. (CHICORY): Cult. CGH & JLM; Müller; Lincs. 1963; frequent. Also cultivated in gardens and on an agricultural scale.

Cnicus benedictus L.: Cult. CGH.

Coreopsis schimperi O. Hoffm. (*C. abyssinica*): Cult. CGH. Very difficult to raise to maturity and therefore unlikely to occur as a casual in Britain.

Cosmos bipinnatus Car.: Cult. CGH; tips; occasional.

Crepis nicaeensis Balbis: gardens; sporadic.

Galactites tomentosa Moench: Cult. FH.

Galinsoga ciliata (Raf.) S. F. Blake: Cult. FH. Frequent on tips but probably from other sources.

GUIZOTIA ABYSSINICA (L. f.) Cass. (NIGER): Cult. CGH & JLM; Müller; Hovda; Lincs. 1956; frequent. A staple bird food included in many bird seed mixtures.

Hedypnois cretica (L.) Dum.-Courset (*H. rhagadioloides* (L.) F. W. Schmidt): Cult. CGH & JLM; Lincs. 1964; occasional.

HELIANTHUS ANNUUS L. (SUNFLOWER): Cult. CGH & JLM; Müller; Hovda; Lincs. 1955; tips; very frequent. The seeds are regularly used as parrot food and also incorporated in food for small mammals such as gerbils.

H. tuberosus L.: Cult. FH.

Iva xanthifolia Nutt.: Cult. DNT; tips; sporadic.

Lactuca saligna L.: Cult. CJJ; Müller.

L. SATIVA L. (LETTUCE): Cult. CGH & JLM; Müller; frequent. Also grown as a garden vegetable.

L. virosa L.: Cult. CGH.

Mantisalca salmantica (L.) Briq. & Cavillier (*Centaurea salmantica* L.): Cult. CGH; Lincs. 1953; sporadic.

Matricaria maritima L.: Cult. CGH; Müller.

Picris echioides L.: Cult. CGH & JLM; Müller; Lincs. 1955; frequent.

P. sprengerana (L.) Poiret: Müller; Lincs. 1955; sporadic.

Rhagadiolus stellatus (L.) Gaertner: Cult. CGH & JLM; Müller; Lincs. 1956; tips; gardens; sporadic. Easily overlooked as it is inconspicuous except in fruit.

Scolymus hispanicus L.: Cult. CGH & JLM; Lincs. 1953; sporadic.

Senecio squalidus L.: Cult. CGH.

S. sylvaticus L.: Cult. CGH.

S. viscosus L.: Cult. FH.

Silybum marianum (L.) Gaertner: Cult. CGH & JLM; Müller; tips; infrequent. An attractive biennial which can persist for several years.

Sonchus asper (L.) Hill subsp. *glaucescens* (Jordan) Ball: Cult. CGH; Müller; Hovda.

S. tenerrimus L.: gardens; sporadic.

Tolpis barbata (L.) Gaertner: gardens; sporadic.

Tragopogon hybridus L. (*Geropogon glaber* L.): Cult. CGH & JLM; Müller; Lincs. 1955; sporadic. The long, needle-like fruits are frequent in Mediterranean seed but they are easily separated during cleaning, hence the plant is rather scarce as a weed.

Verbesina encelioides (Cav.) Benth. & Hook. f. ex A. Gray: Cult. FH.

Wedelia glauca (Ort.) Hoffm. ex Hicken: Cult. CGH, FH & CJJ. Spreads by rhizomes in cultivation.

Xanthium spinosum L.: Cult. JLM; Lincs. 1965; occasional. Much more characteristic as a wool alien.

Liliaceae

Ornithogalum sp: Cult. CGH but not yet grown to maturity.

Juncaceae

Juncus effusus L.: Cult. CGH.

Gramineae

Alopecurus myosuroides Hudson: Cult. CGH; Müller; Lincs. 1956; tips; infrequent.

Apera spica-venti (L.) Beauv.: Cult. CJJ.

Arthraxon hispidus (Thunb.) Makino var. *cryptatherus* (Hack.) Honda: Cult. CGH.

Avena fatua L.: Cult. CGH & JLM; Müller; Hovda; frequent.

A. nuda L. (*A. strigosa* var. *nuda* (L.) Hausskn.): Cult. CGH.

A. SATIVA L. (CLIPPED OATS): Cult. CGH & GDW; Müller; Hovda; tips; frequent.

Beckeropsis nubica (Hochst.) Figari & De Notaris: Cult. CGH & GDW. Cultivated from impurities in imported Ethiopian Niger seed. This and the following species are difficult to raise and would be unlikely to occur as aliens in Britain.

B. petiolaris (Hochst.) Figari & De Notaris: Cult. CGH.

Beckmannia syzigachne (Steudel) Fern.: tips; sporadic.

Brachiaria eruciformis (Sm.) Griseb.: Cult. CGH; tips; sporadic.

B. platyphylla (Griseb.) Nash: Cult. CGH; tips; occasional.

Brachypodium distachyon (L.) Beauv.: Cult. CGH; Müller; Lincs. 1964; occasional.

B. sylvaticum (Hudson) Beauv.: Cult. CGH; tips; sporadic.

Briza minor L.: Cult. CJJ.

Bromus arvensis L.: Cult. FH; Müller.

B. japonicus Thunb.: gardens; sporadic.

B. lanceolatus Roth: Cult. CJJ; tips; occasional.

B. madritensis L.: Cult. CGH; tips; occasional.

B. tectorum L.: Cult. FH; Müller.

B. willdenowii Kunth (*B. unioloides* H. B. K.): Cult. CGH & JLM; Müller; Lincs. 1956; gardens; occasional.

Cenchrus incertus M. A. Curtis (*C. pauciflorus* auct. non Benth.): Cult. CGH. Fruits occur frequently among millet and other seed imported from the Americas but the plant is a rare weed.

Cynodon dactylon (L.) Pers.: Cult. CGH; tips; occasional.

Dactylis glomerata L.: Cult. CGH. Also occurs as a native.

Dactyloctenium aegyptium (L.) Beauv.: Cult. CGH.

Digitaria ciliaris (Retz.) Koeler (*D. adscendens* (H.B.K.) Henrard): Cult. CGH; tips; occasional.

D. ischaemum (Schreber) Muhl.: Cult. CGH & CJJ; gardens; sporadic.

D. sanguinalis (L.) Scop.: Cult. CGH & JLM; Müller; Lincs. 1969; tips; occasional. Similar to, and easily confused with, *D. ciliaris*.

D. ternata (A. Rich.) Stapf.: Cult. CGH.

Diplachne uninerva (Presl) Parod.: tips; sporadic.

Echinaria capitata (L.) Desf.: Cult. CJJ.

Echinochloa colonum (L.) Link: Cult. CGH; Müller; Lincs. 1963; tips; occasional.

E. crus-galli (L.) Beauv.: Cult. CGH & JLM; Müller; Hovda; Lincs. 1955; tips; frequent.

E. frumentacea Link: Cult. CGH.

E. UTILIS Ohwi & Yabano (*E. FRUMENTACEA* auct. non Link) (JAPANESE MILLET): Cult. CGH & JLM; Lincs. 1965; very frequent. An Asian cereal which is a common weed on rubbish tips.

Eleusine africana K. O'Byrne: Cult. FH; tips.

E. indica (L.) Gaertner: Cult. CGH; tips; occasional.

E. tristachya (Lam.) Lam.: gardens; sporadic.

Eragrostis cilianensis (All.) F. T. Hubbard: Cult. CGH; tips; occasional.

E. neomexicana Vasey: Cult. CGH; tips; sporadic.

E. pilosa (L.) Beauv.: tips; sporadic.

E. tef (Zucc.) Trotter: Cult. CGH & GDW; tips; occasional.

E. virescens J. & C. Presl: Cult. CGH.

Gastridium ventricosum (Gouan) Schinz & Thell.: Cult. CGH & JLM.

Hainardia cylindrica (Willd.) Greuter (*Monerma cylindrica* (Willd.) Cross & Dur.): Cult. CGH & JLM; Lincs. 1956; tips; occasional.

HORDEUM DISTICHON L. (BARLEY): Cult. CGH; Müller; Hovda; frequent.

H. jubatum L.: Cult. FH. Often becomes established on waste ground. Also introduced in grass seed.

H. VULGARE L. (BARLEY): Cult. CGH & GDW; Müller; Hovda; very frequent.

Hyparrhenia anthristirioides (A. Rich.) Stapf: Cult. CGH. Cultivated from impurities in Ethiopian Niger seed but unlikely to occur as a weed in Britain.

Lagurus ovatus L.: Cult. CJJ.

Lolium multiflorum Lam.: Cult. CGH & JLM; Müller; Hovda; Lincs. 1953; very frequent.

L. multiflorum Lam. × *L. temulentum* L.: tips; sporadic.

L. perenne L.: Cult. CGH & JLM; Müller; Hovda; very frequent.

L. remotum Schrank: Cult. CGH; Müller.

L. rigidum Gaudin: Cult. CGH; Lincs. 1956; tips; sporadic.

L. temulentum L.: Cult. CGH & JLM; Müller; Hovda; Lincs. 1956; frequent. Usually introduced with seed from the Mediterranean countries.

Microstegium vimineum (Trin.) A. Camus.: Cult. CGH.

Oplismenus hirtellus (L.) Beauv.: Cult. CGH. Cultivated regularly from impurities in Ethiopian Niger seed.

ORYZA SATIVA L. (PADDY RICE): Cult. CGH; Müller. Used as a bird food with the husk still surrounding the grains. Unlikely to occur as a weed in Britain.

Panicum capillare L.: Cult. CGH & JLM; tips; occasional. Usually introduced with millet from the U.S.A.

P. dichotomifolium Michx: tips; sporadic.

P. effusum R. Br.: tips; sporadic.

P. laevifolium Hack.: Cult. CGH; Lincs. 1965; occasional.

P. MILIACEUM L. (BROOMCORN MILLET): Cult. CGH & JLM; Müller; Hovda; Lincs. 1955; very frequent. A staple food for birds used in a number of different colour varieties, e.g. red, yellow and white. By far the commonest bird seed alien on tips.

Parapholis strigosa (Dumort.) C. E. Hubbard: Cult. CGH. Very similar in appearance to *Hainardia*.

Pennisetum glabrum Steud.: Cult. CGH.

Phalaris aquatica L. (*P. tuberosa* L.): Cult. FH & CJJ.

P. brachystachys Link: Cult. CGH; tips; sporadic.

P. CANARIENSIS L. (CANARY GRASS): Cult. CGH & JLM; Hovda; Lincs. 1953; tips; very frequent. A most important species for cage birds. The seeds are included in most commercial mixtures for budgerigars and canaries.

P. minor Retz.: Cult. FH; Lincs. 1953; occasional.

P. paradoxa L.: Cult. CGH & JLM; Müller; Lincs. 1955; gardens; infrequent. Regularly imported with Moroccan Canary Grass seed.

Phleum pratense L.: Cult. CGH.

Piptatherum miliaceum (L.) Cosson (*Oryzopsis miliacea* (L.) Benth. & Hook. f.): Cult. FH.

Poa annua L.: Cult. CGH.

Polypogon monspeliensis (L.) Desf.: Lincs. 1963; tips; occasional.

SECALE CEREALE L. (RYE): Cult. CGH & JLM; Müller; Hovda; Lincs. 1956; frequent.

Setaria faberi Herrm.: Cult. CGH; tips; gardens; occasional. Probably introduced with millets from the U.S.A.

S. geniculata (Lam.) Beauv.: Cult. CGH; Müller; tips; gardens; occasional. Introduced with millets from the U.S.A.

S. ITALICA (L.) Beauv. (MILLET SPRAY, PANICUM MILLET): Cult. CGH & JLM; Müller; Hovda; Lincs. 1953; frequent. Usually sold as an intact inflorescence but sometimes incorporated into mixtures as loose seed, hence the two commercial names.

S. macrostachya H. B. K.: Cult. CJJ.

S. pumila (Poiret) Schultes (*S. glauca* (L.) Beauv.): Cult. CGH & JLM; Müller; tips; infrequent.

S. sphacelata (Schumacher) Stapf & Hubbard: Cult. CGH. Another African plant introduced with Ethiopian Niger seed.

S. verticillata (L.) Beauv.: Cult. CGH; tips; gardens; sporadic.

S. viridis (L.) Beauv.: Cult. CGH & JLM; Müller; Hovda; Lincs. 1955; very frequent. An impurity in many types of seed, it may persist for a few years in places.

SORGHUM BICOLOR (L.) Moench. (*S. SACCHARATUM* (L.) Pers.) (RED DARI): Cult. CGH & JLM; Müller; tips; infrequent. Used in wild bird food mixtures.

S. halepense (L.) Pers.: Cult. CGH, JLM & GDW; Müller; tips; occasional. May persist for several years.

Sporobolus panicoides (Hochst.) A. Rich.: Cult. CGH. Another exotic grass from Ethiopia which is difficult to raise successfully.

TRITICUM AESTIVUM L. (*T. VULGARE* Vill.) (WHEAT): Cult. CGH, JLM & GDW; Müller; Hovda; frequent.

Urochloa panicoides Beauv.: Cult. CGH; Lincs. 1955; occasional.

ZEA MAYS L. (SWEETCORN): Cult. CGH & JLM; Müller; tips; frequent. Used both as a bird food and in pet food for small mammals.

Cyperaceae

Carex demissa Hornem.: Cult. CGH.

ACKNOWLEDGMENTS

The authors are indebted to all those who have contributed to this study. In particular we wish to thank J. E. Haith Ltd and Petfoods Ltd who generously supplied seed samples, including the waste from seed cleanings. We also wish to thank D. McClintock, Dr J. G. Dony and the late J. E. Lousley for their encouragement and helpful suggestions. We are most grateful to Dr G. D. Watts, C. J. Jenness and Mrs F. Houseman for the records from their own work which we have incorporated here. Finally we are most grateful to E. J. Clement for his invaluable assistance, encouragement and suggestions, for identifying many of the more obscure plants and for checking our manuscript.

REFERENCES

Byles, B. D. (1968). Foodstuffs for birds. *Cage Aviary Birds*, **133**: 336–337.
Clapham, A. R., Tutin, T. G. & Warburg, E. F. (1962). *Flora of the British Isles*, 2nd ed. Cambridge.
Gibbons, E. J. (1975). *The flora of Lincolnshire*. Lincoln.
Hayward, I. M. & Druce, G. C. (1919). *The adventive flora of Tweedside*. Arbroath.
Hovda, J. T. (1978). Adventitious plants dispersed as bird seeds. *Blyttia*, **36**: 17–18.
Lousley, J. E. (1953). The recent influx of aliens into the British flora, in Lousley, J. E., ed. *The changing flora of Britain*, pp. 140–159. Oxford.
Lousley, J. E. (1961). A census list of wool aliens found in Britain, 1946–60. *Proc. bot. Soc. Br. Isl.*, **4**: 221–247.
McClintock, D. (1967). All from bird seed. *The Countryman*, **68**: 417–420.
McClintock, D. (1972). What the birds don't eat. *New Scientist*, **55**: 342–343.
Mason, J. L. (1971). Foreigners in the garden. *Country Life*, **150**: 1192–1193.
Mason, J. L. (1973–76). Bird seed aliens, 1–10. *Wild Flower Mag.*, **368–377**.
Müller, K. (1950). Die Vogelfutterpflanzen. *Mitt. Ver. Math. Naturw, Ulm*, **23**: 3–33.
Sandwith, C. I. (1933). The adventive flora of the port of Bristol. *Rep. botl Soc. Exch. Club Br. Isl.*, **10**: 314–363.
Watts, N. S. & Watts, G. D. (1979). Norwich bird seed mixtures and the casual plants of Harford tip. *Trans. Norfolk Norwich Nat. Soc.*, **25**: 1, 300–309.

(*Accepted February 1984*)

Watsonia, **15**, 253–259 (1985)

The ecology and distribution of *Carex chordorrhiza* L. fil.

S. E. PAGE and J. O. RIELEY

Department of Botany, The University, Nottingham, NG7 2RD

ABSTRACT

The vegetation and habitat of the two British localities of *Carex chordorrhiza* are described. Both sites are transition mires in northern Scotland, on which *C. chordorrhiza* grows as a component of low-sedge lawns and shallow pools. *C. chordorrhiza* is a circumpolar, continental plant of boreal and subarctic regions. In the centre of its distribution it is a common plant of a wide range of transition mire communities, but in Britain, central and southern Europe it only survives as a rare glacial-relict species, usually of montane regions.

INTRODUCTION

Carex chordorrhiza L. fil. is a glabrous, extensively creeping, rhizomatous perennial. The rhizomes are up to 1 m in length, with an ascending, non-flowering shoot at each node and a terminal, erect flowering stem. The leaves are narrow (1–2 mm wide), often inrolled, up to 40 cm in length, but much shorter and fewer on the flowering stems. The inflorescence is ovoid, 1 cm long, consisting of 2–5 few-flowered contiguous spikes which are male above and female below.

It was first found in 1897 by the Rev. E. S. Marshall and W. A. Shoolbred at the head of Loch Naver, Altnaharra, Sutherland, v.c. 108 (now Caithness district) and has since been found in several other places within a three mile [5 km] radius of there (Jermy, Chater & David 1982). Until recently, these were the only known localities for this sedge in Britain. However, on a visit by the authors to Insh Fens, Invernesshire, v.c. 96 in July 1978, several large healthy stands of *C. chordorrhiza*, comparable in extent to the Altnaharra populations, were discovered.

This paper presents the results of brief ecological studies carried out at the two British locations for this rare sedge during a return visit to both Caithness and Invernesshire in September 1979. The distribution, phytosociology, ecology and present status of *C. chordorrhiza* in Great Britain and Europe are also discussed.

SITES

INSH FENS

Insh Fens lie within the flat valley floor of the River Spey between Kincraig and Kingussie at an altitude of c.220 m (GR 28/80.03). Part of this area has been drained and reclaimed for pasture, but approximately 3 km^2 of wet fenland still remain. The gradient of the River Spey at this point is very gradual and the river meanders across a wide floodplain, although some attempt has been made to minimize the flooding by the construction of levées. The local geology is mainly hard, acidic quartz, feldspar and schist of the Dalradian and Moinian Series, although in the upper valley of the River Spey, near Laggan, there are outcrops of limestone from which the river gains a small degree of enrichment. Insh Fens and Loch Insh, which lies at the north-eastern end of the fens, are both classified as Grade 1 nature conservation sites (Ratcliffe 1977) for the range of hydroseral communities and associated wetland bird populations that they support.

A large part of the fen vegetation is dominated by a mosaic of tall sedges (*Carex aquatilis**, *C. vesicaria* and *C. rostrata*), rooted in deep water, interspersed with lawns of lower-growing sedges (*C. chordorrhiza*, *C. nigra* and *C. lasiocarpa*) in areas where the water-table is at or just below the surface throughout the summer. There are, in addition, small pools and lochans with floating-leaved and emergent vegetation (mainly *Potamogeton* spp., *Utricularia intermedia*, *Equisetum fluviatile*, *Menyanthes trifoliata* and, occasionally, *Hippuris vulgaris*); dense reed beds of *Phragmites australis*

*Nomenclature follows Clapham, Tutin & Warburg (1981) for vascular plants and Corley & Hill (1981) for bryophytes.

and *Phalaris arundinacea*; patches of willow carr (*Salix cinerea*, *S. aurita* and *S. fragilis*); and, in areas where fen peat accumulation has raised the surface above the winter flood level of the River Spey, ombrotrophic mire communities.

Carex chordorrhiza occurs in abundance in the wet hollows of the low-sedge sward in which *Carex nigra*, *C. lasiocarpa*, *C. rostrata*, *Juncus effusus* and *Equisetum fluviatile* are abundant. Associated emergent herbs include *Menyanthes trifoliata*, *Potentilla palustris*, *Galium palustre*, *Epilobium palustre*, *Cardamine pratensis*, *Myosotis scorpioides* and *Potamogeton polygonifolius*. The principal bryophytes are *Sphagnum auriculatum*, *Calliergon cuspidatum*, *Rhizomnium punctatum* and *Pellia epiphylla* in the wet hollows, and low hummocks of *Sphagnum recurvum* and *S. squarrosum*.

ALTNAHARRA FEN

This mire, which is a Site of Special Scientific Interest, is situated at an altitude of c.80 m in the valley of the River Mudale at the north-western end of Loch Naver. The main section of the mire extends over an area of approximately 1×0.5 km to the west of the A836 Lairg-Tongue road (GR 29/56.36), with smaller areas of fen near the entrance of the River Mudale into Loch Naver (GR 29/577.354), and on the bank of Alltan Buidhe, a tributary of the R. Mudale (GR 29/571.359). The region is one of hard, acidic rocks (quartz, feldspar, gneiss) of the Moinian and Lewisian series with occasional local igneous intrusions of epidiorite, hornblende schist and serpentine.

The water which irrigates the fen is derived from two sources: flood water from the River Mudale and spring water, which originates along the valley side to the north of the fen. Water flows across the fen in a south-easterly direction from the marginal springs and flushes, through surface pools and channels into the River Mudale. Further up-river the mire has been drained to provide poor pasture.

The fen is a mosaic of open water pools and low-sedge communities, but, apart from occasional sparse stands of *Phragmites australis*, large beds of tall reeds and sedges are absent. *Carex chordorrhiza* does not occur in the deeper pools, but it is a constant and abundant species of the flushed channels and shallow pools, where it grows together with *Carex lasiocarpa*, *C. limosa*, *C. rostrata*, *Equisetum fluviatile*, *Menyanthes trifoliata*, *Potamogeton polygonifolius*, *Sphagnum auriculatum* and occasional stunted plants of *Phragmites australis*. The low ridges and hummocks between the pools consist mainly of the mosses *Sphagnum auriculatum*, *S. recurvum*, *S. papillosum*, *S. subnitens* and *Aulacomnium palustre*. Cyperaceous species which occur in these slightly elevated situations are *Carex chordorrhiza*, *C. panicea*, *C. echinata* and *Eriophorum angustifolium*, frequently together with *Molinia caerulea* and *Myrica gale*. In one place stunted bushes of *Salix aurita* were growing on these raised areas.

VEGETATION DESCRIPTION

Descriptions of vegetation stands containing *Carex chordorrhiza* were made at Insh Fens (relevés 3 and 5–11 inclusive) and Altnaharra Fen (relevés 1,2,4, and 12–30 inclusive) using the Braun-Blanquet scale of cover abundance and a plot size of 1 m^2. These data are presented in Table 1, following rearrangement to illustrate the gradient of vegetation types within which *C. chordorrhiza* was found.

Three distinct groups of quadrats are apparent: A (relevés 1–5), B (relevés 6–11) and C (relevés 13–30). Relevé 12 appears to be intermediate between groups B and C. Group A comprises species characteristic of shallow, mesotrophic, open-water pools, whereas species in Group B are more typical of wet, herb-rich, low sedge swamp. Relevés of this second type were recorded only at Insh Fens. The species in the third group are characteristic of more ombrophilous situations than the first two, as exemplified by the increased abundance of *Sphagnum* spp., including *S. auriculatum*, *S. papillosum* and *S. subnitens*. All the relevés in this last group were recorded at Altnaharra.

CHEMICAL ANALYSIS

Water samples were collected at both sites and, on return to the laboratory, these were filtered and analysed for calcium, magnesium, sodium, iron, manganese, and potassium ions by atomic absorption spectrophotometry. pH was also measured. The analysis results for stands containing *C. chordorrhiza* are presented in Table 2.

TABLE 1. VEGETATION DESCRIPTIONS OF STANDS CONTAINING *CAREX CHORDORRHIZA*

Digits are those of the Braun-Blanquet scale of cover-abundance. Relevés 3 and 5–11 inclusive: Insh Fens; Relevés 1, 2, 4 and 12–30 inclusive: Altnaharra Fen.

Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Number of species	7	5	5	5	6	13	10	12	10	11	12	5	11	11	7	7	6	9	7	9	7	9	7	10	8	6	8	6	11	10
Carex chordorrhiza	3	3	4	1	4	3	2	4	2	2	3	3	2	2	3	2	3	3	3	3	2	3	2	2	4	4	2	3	2	2
Menyanthes trifoliata	1		3		3	2	3	3					1	2	+	1	+	+	+	+	1	+		2			1		+	2
Potamogeton polygonifolius	+	2	2	3	2	+							2	2	3	3	2	2	2	2		1	2	2					+	
Carex lasiocarpa		2		1		3	2								2	2		1	1			1	1							
Carex rostrata	2	1								1		3	1	2																
Equisetum fluviatile		1	2	1	2	3	4	3	4	2	3	+	+	+																
Potentilla palustris					+	1		1	2	1	1	+																		
Galium palustre							1	+	2	1	2																			
Myosotis scorpioides						+			1	1	2																			
Cardamine pratensis						+		1			1																			
Filipendula ulmaria						+	2	1																						
Pellia epiphylla						2	2																							
Calliergon cuspidatum						1	1																							
Sphagnum squarrosum										5	3																			
Agrostis stolonifera									+	+																				
Epilobium palustre						+			+																					
Rhizomnium punctatum								+			1																			
Mentha aquatica									1	2																				
Caltha palustris									+		+																			
Juncus effusus									2	2																				
Sphagnum auriculatum												2	2		+	+	3	2	5	3	4	4	1	3	2	3		3	2	
Molinia caerulea													1	1				+		+	2	1	1	2	2	2		2	+	+
Eriophorum angustifolium													+	1		+		+		+		1					+		2	1
Myrica gale	1															+	+	+	+		1			2	2		3	1		
Carex echinata														+						+		+			2				2	
Drosera rotundifolia													+											+				+		+
Aulacomnium palustre																		+									2		+	+
Sphagnum papillosum																											4	2	2	2
Sphagnum subnitens																													2	2
Eleocharis multicaulis	2														1		2		+	+										
Carex nigra					1		1	1						1													2			
Carex panicea																					2	1			2					
Sphagnum recurvum											3													2	2	2				
Ranunculus flammula								1			+														1					

Additional species:
1: *Nymphaea alba* (1); 3: *Rhynchospora alba* (1); 4: *Phragmites australis* (1); 6: *Bryum pseudotriquetrum* (+); 7: *Chiloscyphus polyanthos* (1); 8: *Campylium stellatum* (1), *Scorpidium scorpioides* (1); 10: *Festuca ovina* (+); 11: *Marchantia polymorpha* (3); 13: *Carex limosa* (2), *Juncus bulbosus* (+); 14: *Juncus articulatus* (1), *J. bulbosus* (2); 15: *Deschampsia flexuosa* (+); 20: *Drosera anglica* (+); 21: *Erica tetralix* (1); 23: *Narthecium ossifragum* (2), *Phragmites australis* (+); 24: *Carex pulicaris* (+), *Erica tetralix* (+); 26: *Pedicularis palustris* (1), *Viola palustris* (+); 27: *Drosera anglica* (+); 29: *Salix aurita* (2); 30: *Juncus articulatus* (2), *Salix aurita* (2).

TABLE 2. CHEMICAL COMPOSITION OF SURFACE WATERS FROM STANDS OF *CAREX CHORDORRHIZA*

Relevés 9 and 10: Insh Fens; relevés 14 and 15: Altnaharra Fen. Values are expressed as mg l^{-1} for cations; n.d. not detectable.

Relevé	pH	Ca	Mg	Na	Fe	Mn	K
9	5.9	4.1	1.5	8.5	0.6	n.d.	0.7
10	5.6	2.7	1.0	9.4	0.1	n.d.	0.2
14	5.4	1.1	2.2	12.5	5.6	0.7	0.3
15	6.5	2.3	1.1	7.0	0.2	n.d.	0.1

DISCUSSION

Carex chordorrhiza is a circumpolar, continental plant of boreal and subarctic regions (Meusel *et al.* 1965) (Fig. 1). It is common at low and middle altitudes throughout most of Iceland, Scandinavia, Finland and the USSR as far east as western Siberia, but it is of less frequent occurrence in the arctic-boreal zones of North America and Asia. Within temperate America and Europe its distribution is sporadic and, for the most part, restricted to mountainous districts, e.g. the foothills of the Bavarian Alps (Oberdorfer 1949, Kaule 1972) and the Jura and Massif Central of France (Fournier 1946). In these more southerly locations, *C. chordorrhiza* is an uncommon to rare species which may have disappeared from many of its former localities as a result of drainage (Hultén 1962). In these situations it is considered a glacial relict species by Oberdorfer (1957), who described the Caricetum chordorrhizae (Paul & Lutz 1941) as being a very rare, arctic-continental relict association within Southern Germany, and by Szafer (1966) in Pomerania, Poland. *C. chordorrhiza* has been recorded as a constituent of sub-fossil peat deposits in Central and Northern Europe excluding the British Isles (Tallis & Birks 1965, Rybníček 1972). The species composition of these sub-fossil communities is similar to many of the present day mire communities containing *C. chordorrhiza*.

Throughout Europe *C. chordorrhiza* is a constituent of the vegetation of transition mires, i.e. mesotrophic peatlands (poor fen) which are intermediate between eutrophic, mineral-rich mires (rich fen) and oligotrophic, nutrient-poor sites (e.g. raised mire). Characteristically it occurs in low sedge vegetation of the class Parvocaricetea†, within both the orders Caricetalia nigrae and the more eutrophic Tofieldietalia. Less frequently *C. chordorrhiza* has been noted as a constituent of the class Phragmitetea (tall sedge vegetation). Kulczynski (1949) seeks to explain this wide ecological tolerance of varying water depth and nutrient status in terms of the rooting depth of this and similar transition mire species. Unlike large emergent plants, which root in deep mineral or peat sediments and tolerate partial submergence during oscillations of the water table, the small members of the Cyperaceae (e.g. *C. chordorrhiza* and *C. limosa*) root in higher, light peat turfs. These species avoid submergence by floating to the surface together with the substrate. Damman (1963) notes that the cord-like stems of *C. chordorrhiza* may be seen growing almost vertically to keep up with peat growth, and this feature of the ecology of this sedge may help to explain how it can survive into the final stages of the succession from transition to ombrotrophic mire vegetation.

In Scandinavia and Finland, *C. chordorrhiza* forms a component of the low-sedge vegetation of transition mires and the sedge dominated 'flarks' (wide, elongate pools) of raised mires. Commonly associated cyperaceous species include most of those already listed for the Scottish sites, in addition to *Carex curta*, *C. dioica*, *Eriophorum vaginatum*, *Trichophorum cespitosum* and the more northerly species *Carex magellanica* and *C. saxatilis*. Additional species include small herbaceous plants, e.g. *Menyanthes trifoliata* and *Potentilla palustris*; ericoids, notably *Andromeda polifolia*, *Vaccinium uliginosum* and *V. oxycoccos*; and low shrubs of willow (e.g. *Salix lapponum*) and *Betula nana*. The moss layer contains various *Sphagnum* spp. including *S. teres*, *S. contortum*, *S. warnstorfii*, *S. lindbergii* and *S. squarrosum*, but in more calcareous situations brown mosses assume a greater importance. They include *Scorpidium scorpioides*, *Campylium stellatum*, *Cinclidium stygium*,

---

†Phytosociological classification follows Westhoff & den Held (1969).

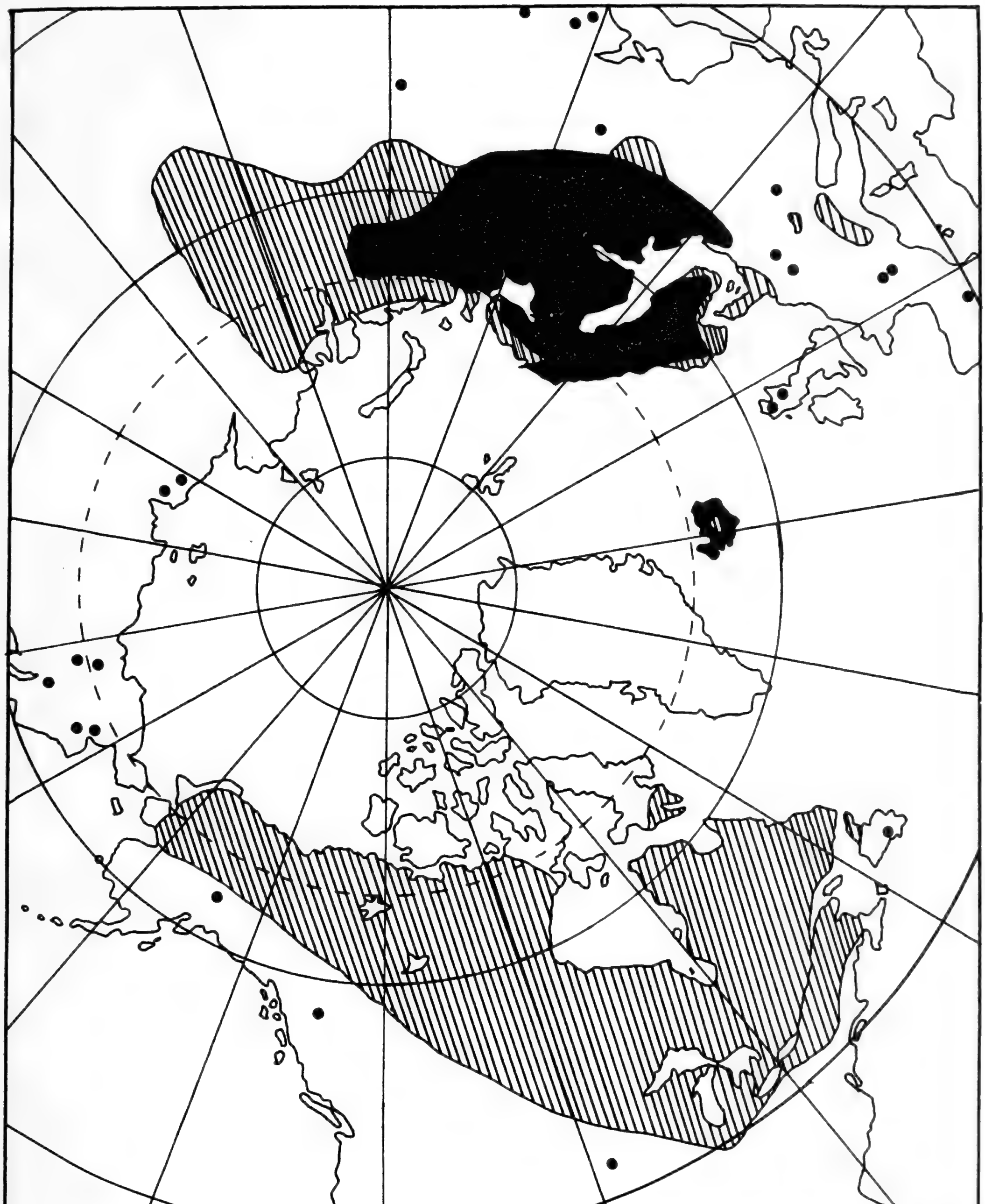


FIGURE 1. The distribution of *Carex chordorrhiza* after Meusel *et al.* (1965) and Hultén (1962; 1971). The solid shading represents the area in which *C. chordorrhiza* is abundant; the hatching, areas in which it is of less frequent occurrence; solid circles, isolated sites.

Meesia triquetra and species of *Drepanocladus* and *Calliergon* (Christophersen 1925; Nordhagen 1928, 1943; Sjörs 1948; Dahl 1956; Malmer 1965; Persson 1965; Eurola & Vorren 1980).

In Eastern Poland and Polesie (now part of western Russia) *C. chordorrhiza* is recorded from a range of transition mire communities, including both orders of the Parvocaricetea and also the wetter Magnocaricion (tall sedge) fen vegetation of the Phragmitetea (Kulczynski 1949, Pałczynski 1975). The dominant species in the latter community are *Carex vesicaria*, *C. elata* and *Phragmites australis*, with smaller sedges such as *C. chordorrhiza* and herbaceous species forming a lower secondary layer.

In most of central and southern Europe, *C. chordorrhiza* is extremely rare or absent, but in the foothills of the Bavarian Alps it occurs as an occasional component of transition mire vegetation, both within the communities of the Parvocaricetea and, as in Poland, the Phragmitetea (Kaule 1972).

On the Scottish sites, stands containing *C. chordorrhiza* would appear to lie entirely within the low-sedge mires of the order Caricetalia nigrae of the Parvocaricetea. Only Relevé 8 contained species more typical of the Tofieldietalia (namely *Scorpidium scorpioides* and *Campylium stellatum*).

This wide range of plant communities from which *C. chordorrhiza* is recorded in Europe is also reflected in the range of pH values of surface waters and peats, and the following have been recorded by various workers.

Norway:	pH 3.6–6.7	(surface peats)	(Christophersen 1925)
Poland:	pH 4.6–5.0	(surface peats)	(Pałczynski 1975)
Sweden:	pH 4.8–6.4	(surface waters)	(Sjörs 1948)
Scotland:	pH 5.4–6.5	(surface waters)	(see Table 2)

Communities of the Caricetalia nigrae usually have a mire water pH lower than 5.5–6.0 and those of the Tofieldietalia greater than 5.5. At the top of the range, a surface water pH of 7.2 was recorded for a spring mire community containing *C. chordorrhiza* in Finland by Lahermo *et al.* (1977). The pH of the water samples from the Scottish sites is in the upper range for this species in Europe (pH 5.4–6.5). Calcium, magnesium, sodium and potassium contents are low, however, and these waters can only be regarded as moderately mesotrophic. Except for a high iron content in one of the Altnaharra samples, the waters from both sites are similar in pH and cation content.

In the course of the study of *C. chordorrhiza* in its two known localities in the British Isles, several other transition mires in northern Scotland were visited. Although these had habitat conditions and plant associations similar to those at both Altnaharra and Insh, *C. chordorrhiza* was absent. Since the general nature of the vegetation of the Altnaharra and Insh sites is no different from that at many others within the region, their uniqueness rests solely upon the presence of fairly large populations of one rare sedge.

Undoubtedly many fenland sites have been reduced in size or destroyed through drainage and converted to agricultural land within recent history. However, this cannot account entirely for the infrequent occurrence of *C. chordorrhiza* in northern Britain, for throughout most of its distributional range in northern Europe this sedge occurs within plant associations which are essentially the same as those in which it grows at Altnaharra and Insh Fens. In common with other rare species of British mires, such as *Schoenus ferrugineus* (Wheeler, Brookes & Smith 1983), *C. chordorrhiza* can be considered to be a glacial relic, which was left behind during the northward retreat of boreal species at the end of the last glaciation and, as such, can be regarded as part of the Northern Montane Element of the British flora (Matthews 1955).

ACKNOWLEDGMENTS

We wish to express our thanks to Professor G. Kaule, University of Stuttgart, for information on the distribution of *Carex chordorrhiza* in southern Europe, and to P. Smithurst and B. Case for technical and photographic assistance, respectively. One of us (S.E.P.) received financial assistance from the Carr Scholarship Fund of the University of Nottingham.

REFERENCES

CHRISTOPHERSEN, E. (1925). Soil reaction in Sylene National Park, Norway. *Trans. Conn. Acad. Arts. Sci.*, **27**: 471–577.

CLAPHAM, A. R., TUTIN, T. G. & WARBURG, E. F. (1981). *Excursion flora of the British Isles*, 3rd ed. Cambridge.

CORLEY, M. F. V. & HILL, M. O. (1981). *Distribution of bryophytes in the British Isles.* Cardiff.

DAHL, E. (1956). Mountain vegetation of Rondane in South Norway and its relation to the environment. *Skr. norske Vidensk-Akad.* **3**: 1–374.

DAMMAN, A. W. H. (1963). *Key to the* Carex *species of Newfoundland by vegetative characteristics.* Canadian Department of Forestry (Publication **1017**).

EUROLA, S. & VORREN, K. D. (1980). Mire zones and sections in North Fennoscandia. *Aquilo, Ser. Bot.*, **17**: 39–56.

FOURNIER, P. (1946). *Les quatres flores de la France.* Paris.

HULTÉN, E. (1962). The circumpolar plants, Vol. 1. *K. svenska Vetensk-Akad. Handl.*, **8** (5).

HULTÉN, E. (1971). *Atlas över Växternas Utbredning i Norden.* Generalstabens Litografiska Anstalts Förlag, Stockholm.

JERMY, A. C., CHATER, A. O. & DAVID, R. W. (1982). *Sedges of the British Isles.* London.

KAULE, G. (1972). Zum Vorkommen von *Carex chordorrhiza* Ehrh. in Bayern. *Ber. bayer. bot. Ges.*, **43**: 77–83.

KULCZYNSKI, S. (1949). Peat bogs of Polesie. *Mem. Acad. Pol. Sci.*, Ser. B., **315**: 1–356.

LAHERMO, P., VALOVIRTA, V. E. & SÄRKIOJA, A. (1977). *The geobotanical development of spring-fed mires in Finnish Lapland.* Geological Survey of Finland, Helsinki (Bulletin **287**).

MALMER, N. (1965). The southern mires. *Acta phytogeogr. suec.*, **50**: 149–158.

MATTHEWS, J. R. (1955). *Origin and distribution of the British flora.* London.

MEUSEL, H., JÄGER, E. & WEINERT, E. (1965). *Vergleichende Chorologie der zentraleuropäischen Flora.* Jena.

NORDHAGEN, R. (1928). *Die Vegetation und Flora des Sylenegebietes.* Oslo.

NORDHAGEN, R. (1943). Sikilsdalen og Norges Fjellbeiter. *Bergens Mus. Skr.*, **22**: 1–607.

OBERDORFER, E. (1949). *Pflanzensoziologische Exkursions Flora für Suddeutschland.* Stuttgart.

OBERDORFER, E. (1957) Süddeutsche Pflanzengesellschaften. *Pflanzensoziologie, Jena*, **10**: 1–564.

PAŁCZYNSKI, A. (1975). Wspolczesna szata roslinna Bagan Jacwieskie (Pradolina Biebrzy). *Roczn. Nauk. roln., Ser. D, Warszawa*, **145**.

PAUL, H. & LUTZ, J. (1941). Zur soziologische-ökologischen Charakterisierung von Zwischenmooren. *Ber. bayer. bot. Ges.*, **25**: 1–28.

PERSSON, A. (1965). Mountain mires. *Acta phytogeogr. suec.*, **50**: 249–256.

RATCLIFFE, D. (1977). *A nature conservation review*, vol. 2. Cambridge.

RYBNÍČEK, K. (1972). A comparison of the present and past mire communities of Central Europe, in BIRKS, H. J. B. & WEST, R. G., eds. *Quaternary Plant Ecology*, pp. 237–261. Oxford.

SJÖRS, H. (1948). Myrvegetation i Bergslagen. *Acta phytogeogr. suec.*, **21**: 1–299.

SZAFER, W. (1966). *The vegetation of Poland.* Oxford.

TALLIS, J. H. & BIRKS, H. J. B. (1965). The past and present distribution of *Scheuchzeria palustris* L. in Europe. *J. Ecol.*, **53**: 287–298.

WESTHOFF, V. & DEN HELD, A. J. (1969). *Plantengemeenschappen in Nederland.* Zutphen.

WHEELER, B. D., BROOKES, B. S. & SMITH, R. A. H. (1983). An ecological study of *Schoenus ferrugineus* L. in Scotland. *Watsonia*, **14**: 249–256.

(*Accepted June 1984*)

Watsonia, **15**, 261–264 (1985)

Dioecism and pollination in *Ruscus aculeatus*

Q. O. N. KAY

Department of Botany and Microbiology,
University College of Swansea, Swansea, SA2 8PP

and

J. PAGE

Les Asphodèles, Rue des Reines, Forest, Guernsey

ABSTRACT

Sex distribution, pollination and fruit set were studied in wild populations of the winter-flowering, normally dioecious shrub *Ruscus aculeatus* L. in Guernsey, South Wales and Oxfordshire. Most plants were either entirely male or entirely female. 41% of plants were female in both Guernsey and South Wales, but 8.4% of the plants in Guernsey and 0.6% in South Wales were andromonoecious, with male flowers as well as some female or hermaphrodite flowers. The Oxfordshire population was 50% male, 50% female. The flowers appear to be structurally adapted to insect pollination, but no insects were observed to visit the flowers of any sex form. Although overall fruit-set on female plants was low, with standing crops of 2.87 berries per female plant in South Wales and 0.5 in Oxfordshire in December 1982, some female plants separated by distances of more than 20 m from the nearest male showed high fruit-set. Hand-pollination also gave high fruit-set. Male and female plants did not differ significantly in height or clump diameter.

INTRODUCTION

Ruscus aculeatus L. (Butcher's Broom), a small evergreen shrub in the Liliaceae, is locally common as a native plant in woods and coastal scrub in southern England and south-western Wales, usually on base-rich soils. It was once cultivated as a medicinal plant, and is now grown to some extent as an ornamental plant and to provide cover for pheasants; it has been introduced fairly widely, but is slow to naturalize. The plants are slow-growing but very long-lived and may eventually spread vegetatively to form clumps 2 m or more in diameter; most populations consist of fairly well-spaced individual bushes of varying size.

R. aculeatus is widespread in western, southern and south-central Europe, reaching the limits of its range in eastern Europe and central Hungary. It was described as dioecious by Warburg (1962) but as subdioecious by Yeo (1980). We have investigated sex distribution, pollination and fruit set in some wild populations in southern Britain and the Channel Islands.

DIOECISM

The extent to which natural populations of *R. aculeatus* are dioecious, and the means by which it is pollinated, are both uncertain. A long-term study of a population at Bookham Common, Surrey (Hillman & Warren 1973; Hillman 1979) showed that this population was almost completely dioecious, with 104 of a sample of 105 plants that flowered being either completely female (62%) or completely male (37%); the remaining plant was a large male clump that produced a single berry in one year, and was regarded as andromonoecious.

We have studied populations of *R. aculeatus* in three areas; in the Gower Peninsula in Glamorgan, in southern Oxfordshire and in Guernsey. In Gower and Guernsey it fully appears to be native, growing mainly in sea-cliff scrub in Guernsey and in both sea-cliff scrub and nearby limestone woodland in Gower. The Oxfordshire population, in beechwoods on chalk, is certainly very long-established and may be native.

The Gower populations were almost completely dioecious, with 163 of a sample of 164 plants in Crawley and Parkmill Woods being either entirely male (58%) or entirely female (41%). The remaining plant was male-flowered, but bore (in December 1982) a single mature berry on an otherwise male-flowered branch; like the similar plant found by Hillman & Warren at Bookham Common, it may have been subandromonoecious, but no hermaphrodite flowers were observed on it. The small Oxfordshire population of 18 plants consisted of nine (50%) male and nine (50%) female plants scattered over a wide area, in Mapledurham and Chazey Woods. The Guernsey population contained 41% females, 50.6% males and 8.4% of andromonoecious plants in a total sample of 347 plants. The andromonoecious plants bore mature berries, but also had many male flowers as well as some female or hermaphrodite flowers in December 1982 and January 1983.

POLLINATION

The populations of *R. aculeatus* that we have studied flower mainly in winter (from October to April or May). The small inconspicuous flowers, which appear to be adapted for insect rather than wind pollination but have no nectar or other obvious means of attracting pollinators, are usually produced singly on the undersides of the cladodes, with about 10–15 flowers open simultaneously on a plant of normal size during peaks of flowering; each flower remains open for several days. Male and female plants are often separated by distances of several metres.

We did not observe any visits to the flowers by insects, although flowering plants were watched carefully at a variety of times and in a variety of weather conditions from November to March. No pollinating agent was observed during the Bookham Common study either, and it was suggested that the pollinating agent associated with *R. aculeatus* in the Mediterranean region might be absent from Britain. It was also thought that some wind pollination might occur when male and female shoots were intermingled.

Nevertheless, some transfer of pollen over distances of more than 20 m must presumably occur to produce the observed fruit-set in isolated females. For example, the female plant with the highest fruit-set (14 berries) in the Crawley Wood, Gower population was 24 m from its nearest male neighbour. *R. aculeatus* plants are often covered with spider's webs in winter, suggesting the presence of insects, and small and large flies (?*Fannia* sp., *Calliphora* sp., and *Scatophaga stercoraria*) were seen resting on the cladodes on a few occasions, but showing no apparent interest in the flowers. Ladybirds (*Adalia bipunctata* L. and *Coccinella 7-punctata* L.) were often seen hibernating in the shelter of the cladodes. The male and female flowers resemble very closely one another, and are similar in size, structure, surface texture and colour to flowers known to be pollinated by flies or small Hymenoptera (for example those of *Rhamnus catharticus* L.), although there is apparently no nectar and no detectable scent. Seed-set is not or only weakly correlated with the distance to the nearest male plant in the Gower and Bookham Common (Hillman & Warren 1973; Hillman 1979) populations. It seems possible that some pollination may be effected by insects that use the *R. aculeatus* bushes for sleep or shelter (pollination by mechanisms of this type occurs in the orchid *Serapias* and other Mediterranean plants (Dafni *et al.* 1981)) although some sort of deception mechanism may also be involved, with the flowers mimicking insects. Both of these possible pollination mechanisms are unusual and interesting. The frequency of visits to the flowers is likely to differ in different areas, and careful observation of flowering *R. aculeatus* plants by botanists living near wild populations might be very rewarding.

FRUIT SET

R. aculeatus has a very low reproductive capacity; the average seed output per female plant per year is 1–5 in the populations that have been studied. The conspicuous red berries are produced very sparingly; they contain only one or two very large seeds, and take up to a year to mature. The berries appear to be unpalatable, have no obvious means of dispersal apart from gravity, and commonly remain on the plant for months after ripening (Hillman 1979).

Most British populations grow in relatively mild maritime areas, where natural means of pollination and dispersal should be available. General observations of wild populations of *R. aculeatus* in these areas show that some plants produce relatively large numbers of berries (10 or more), while others produce few or none. While this might be the result of selective pollination of some female plants, or of differences in potential fertility between different females, it is also possible that some populations may contain a proportion of monoecious or hermaphrodite plants with higher fruit-set than females. Clones of *R. aculeatus* are known in cultivation (for example 'Treseder's Variety', apparently introduced by Treseders' Nurseries Ltd, Truro, Cornwall, in the late 1950s) which produce berries freely. These clones appear to be andromonoecious (Yeo 1980), although 'Treseder's Variety' is described in the horticultural literature as hermaphrodite. Clones of this type may produce hermaphrodite flowers only in April and May, but male flowers during the rest of the flowering season (P. F. Yeo, pers. comm.).

Average fruit-set was assessed by the standing crop of mature berries in December 1982. It was low in both Gower (2.87 berries per female, n=68) and Oxfordshire (0.5 berries per female, n=9). This is comparable with the figure of 1.8 berries per female plant (n=43) reported by Hillman & Warren at Bookham Common. Fruit-set on females, and also on most andromonoecious plants, in the Guernsey population was not precisely assessed, but was similar to that on females in Gower, with 2–5 berries on many plants but greater numbers on a few plants. A particularly high fruit-set was observed on one andromonoecious plant in Guernsey, with eight berries on a single branch, but some females showed similarly high fertility. In contrast to this, the single presumably andromonoecious plant found in Gower, and the similar plant found by Hillman & Warren (1973) at Bookham Common, each set only a single berry. More work on the fertility of andromonoecious plants is needed. In order to determine the extent to which fruit-set on females was limited by inadequate pollination, female flowers were hand-pollinated on two female plants isolated by 8–10 m from the nearest male plant in Gower, and on one similarly isolated female and one female plant adjacent to a male plant in Oxfordshire, during late December 1982 (Table 1). Crossed and control flowers were marked by coloured cotton threads tied around the bases of the cladodes. The hand-pollinated flowers showed a high fruit-set in all cases, with nil or very low fruit-set on unpollinated flowers on the same plants. The berries took twelve months to mature. The Oxfordshire female next to a male plant showed a considerably higher spontaneous fruit-set than the isolated plants, but it was still very low in comparison with the fruit-set of hand-pollinated flowers. It thus appears that fruit-set is limited by inadequate pollination in these dioecious populations.

TABLE 1. FRUIT-SET IN HAND-POLLINATED FLOWERS OF *RUSCUS ACULEATUS*

Site	% fruit set	
	Hand-pollinated	Control
Gower		
(2 isolated plants)	70 (10 flowers)	0 (10 flowers)
Oxfordshire		
(Isolated plant)	69 (29 flowers)	0.8 (all other flowers)
(Plant next to male)	90 (10 flowers)	13.5 (all other flowers)

The low frequency of andromonoecious plants in the populations that we have investigated suggests that the higher fruit-set that might be expected to result from self-pollination is either not advantageous or is offset by inbreeding depression or some other disadvantage. Self-pollinating andromonoecious plants would however be able to establish populations from single isolated individuals, and might also be at an advantage when cross-pollination was reduced or prevented by other factors. Andromonoecious plants have been reported to be common in some areas of Sussex (D.C. Lang, pers. comm.) and more observations of their frequency in wild populations of *R. aculeatus* are needed.

NICHE PARTITIONING

Theoretical considerations of dioecism suggest that the sexes are likely to differ to some extent in their ecological requirements and their timing of growth, and differences of this type have been found in an increasing number of dioecious species (Freeman *et al.* 1976; Bawa 1980; Cox 1981). Measurements of plant diameter, height and spacing were made in a fairly large population of *R. aculeatus* growing in a sloping woodland site that showed a more or less uniform gradient of habitat factors (North-hill Wood, Gower) in order to determine whether the sexes differed from one another in these parameters (Table 2). No significant differences between the sexes in plant diameter or height were found in this sample (although a larger population would have shown significant differences with similar differences between the means; males had greater mean diameter and height) but the distance between a male plant and its nearest male neighbour was significantly greater than the distance between a female plant and its nearest male neighbour. This might result from sex differentiation, with males competing more intensively with one another than with females. However, it seems more likely to result from poor berry dispersal, with females being closer to their progeny (male and female) than are males.

TABLE 2. MEAN DIAMETER, HEIGHT AND SPACING OF MALE AND FEMALE PLANTS (NORTH-HILL WOOD, GOWER)

	Diameter (centimetres)	Height (centimetres)	Nearest male (metres)	Nearest female (metres)
Males	101.56	86.42	6.96*	11.36
(n=52)	±7.23	±2.73	±0.73	±1.72
Females	91.22	79.28	5.14*	11.00
(n=32)	±9.38	±4.70	±0.68	±1.84

*Significant difference between males and females, $P=0.05$

ACKNOWLEDGMENTS

We are grateful to D. McClintock and Dr P. Yeo for their informative and encouraging discussion of the work, and to Dr A. Lack for his helpful comments on the manuscript.

REFERENCES

Bawa, K. S. (1980). Evolution of dioecy in flowering plants. *A. Rev. Ecol. Syst.*, **11**: 15–39.

Cox, P. A. (1981). Niche partitioning between sexes of dioecious plants. *Am. Nat.*, **118**: 572–577.

Dafni, A., Ivri, Y. & Brantjes, N. B. M. (1981). Pollination of *Serapias vomeracea* Briq. (Orchidaceae) by imitation of holes for sleeping solitary male bees (Hymenoptera). *Acta Bot. Neerl.*, **30**: 69–73.

Freeman, D. C., Klikoff, L. G. & Harper, K. T. (1976). Differential resource utilization by the sexes of dioecious plants. *Science*, **193**: 597–599.

Hillman, E. M. (1979). A study of *Ruscus aculeatus* on Bookham Common. *Lond. Nat.*, **58**: 44–55.

Hillman, E. M. & Warren, A. (1973). Survey of *Ruscus aculeatus* on Bookham Common: the first two years. *Lond. Nat.*, **52**: 93–103.

Warburg, E. F. (1962). *Ruscus*, in Clapham, A. R., Tutin, T. G. & Warburg, E. F. *Flora of the British Isles*, 2nd ed., p. 969. Cambridge.

Yeo, P. F. (1968). A contribution to the taxonomy of the genus *Ruscus*. *Notes R. bot. Gdn Edinb.*, **28**: 237–268.

Yeo, P. F. (1980). *Ruscus* L., in Tutin, T. G. *et al.*, eds. *Flora Europaea*, **5**: 73–74. Cambridge.

(*Accepted June 1984*)

Watsonia, **15**, 265–267 (1985)

The significance of multigerm seedballs in the genus *Beta*

M. F. B. DALE

Scottish Crop Research Institute, Pentlandfield, Roslin, Midlothian, EH25 9RF

and

B. V. FORD-LLOYD

Department of Plant Biology, The University, P.O. Box 363, Birmingham, B15 2TT

ABSTRACT

The presence of multigerm seedballs in the genus *Beta* (Chenopodiaceae) is noted. The distribution of such a multigerm seedball could effectively overcome problems caused by long-distance dispersal and subsequent isolation of such obligately outbreeding species. This hypothesis was tested by assessing the extent of intra-seedball hybridization and successful seed production, which demonstrated that such seedball progenies are interfertile and so can colonize new areas in isolation from the parent populations.

INTRODUCTION

The occurrence of a glomerule containing several seeds is comparatively rare within the angiosperms. Such multigerm seedballs are found in the family Chenopodiaceae in the genera *Spinacia* L. and *Beta* L. Multigermicity within *Spinacia* has been examined previously (Astley & Ford-Lloyd 1981) and it was concluded that this character permits the survival of these dioecious plants following the colonization of new areas occurring outside the pollen range of the parent populations.

In the genus *Beta* a range of breeding behaviour exists encompassing self-fertility and self-incompatibility. The incompatibility system is genetically controlled by a complex gametophytic system governed by at least four loci, each with a number of alleles, and is further influenced by modifying genes (Larsen 1977). A diversity of life-cycles also exists including strict annuals and short-term perennials. The association between life cycle and breeding behaviour will be examined in a future publication.

The wild xenogamous members of *Beta* section *Beta* have a wide and largely littoral distribution. It is known that a large proportion of mature seeds produced by the end of the flowering season are shed in the immediate vicinity of the maternal plant. Eventually individuals establish in the surrounding area and become incorporated into the larger parent population. Some of the seed, however, instead of establishing locally may be dispersed over greater distances.

The major agent of long distance dispersal of the multigerm seedballs is believed to be tidal movements of the sea. Darwin reported in 1855 (cited in Barrett 1977) estimated potential dispersal distances of over several hundred miles and other observations indicated that seed immersed in cold salt water for periods of 30 days still had good levels of germination.

The successful colonization of areas within the Mediterranean region by the self-fertile plants of section *Beta* can be readily understood. Baker (1955) and Stebbins (1957) have both presented a large amount of data supporting the correlation between long-distance dispersal, colonization of isolated areas and self-fertilization in various species of plants.

The *Beta* populations found on shores around the North Sea, including those of the British Isles, and some found around the Mediterranean are largely self-incompatible. Such a breeding system would normally present problems after long distance dispersal and subsequent establishment because an obligately outcrossing individual relies on foreign pollen to effect fertilization. However, it is postulated that the dispersal of a multigerm seedball, as found in the section *Beta*, would effectively overcome this problem. Such a solution would result in the simultaneous establishment of cross-compatible individuals in very close proximity, basically resulting in a small 'founder' population of two to several plants.

Baker (1965) mentioned the case of self-incompatible *Raphanus* species in which the whole fruit is distributed, stating that several seedlings germinate together but that these do not compete with each other so destructively that only one plant attains maturity. He observed that four or five plants could successfully reach maturity, setting reduced numbers of seed. Astley & Ford-Lloyd (1981) found potentially inter-fertile male and female plants arising from the same seedball in the wild, dioecious species of *Spinacia*. While they found competition between individuals from the same seedball, in no case did the competition prevent the plants attaining maturity and setting seed. The present study examines individuals from within the multigerm seedballs (termed seedball population) of *Beta vulgaris* L. and their ability or otherwise to effect cross- and self-pollination.

MATERIALS AND METHODS

The material used in this study, listed in Table 1, was chosen for availability, known outcrossing behaviour and to represent as wide a range of material within *Beta vulgaris* as possible.

Three seedballs per accession were used. The seeds were grown in standard plastic plant pots using John Innes No. 1 compost. The plants were given a vernalization treatment of 6°C with a 16-hour day for seven weeks. The plants were grown 'in situ': plants emerging from individual seedballs were allowed to grow and compete throughout their life cycle. The numbers emerging, establishing and reaching flowering were noted. At the onset of flowering, single branches of all individuals were isolated using bags made of polypropylene non-woven material in order to check on the breeding behaviour of the individual plants. The seedball progenies were also isolated to prevent inter-seedball pollination. This allowed free pollen flow between plants within each seedball population. After flowering was completed the pollination bags were removed and the inflorescences allowed to mature. Seed set was assessed and seedball populations classified accordingly.

RESULTS

The results are presented in Table 1. All plants grew well and flowered at approximately the same time. Competition was observed between the plants within the seedball populations. However this was not sufficient to prevent the weaker individuals from reaching maturity and effecting pollination even when they had reduced stature. It was noted that flower number and pollen production was reduced in the weaker individuals.

Of the 60 multigerm seedballs examined seedling numbers ranged from 2 to 5. All plants examined when individually isolated set no seed indicating that they were self-incompatible. Out of the 60 seedball populations examined, 54 set good seed while six did not. All six seedball populations consisted of two individuals only.

As observed by Astley & Ford-Lloyd (1981) in *Spinacia*, there were marked time differences in the opening of flowers within the multigerm flower cluster, with two to four days between successive flowers opening.

DISCUSSION

The hypothesis that the production of a multigerm seedball can overcome potential problems arising after long-distance dispersal and subsequent isolation of self-incompatible individuals appears to be justified. It is confirmed in the present study that different incompatibility specificities are present within seedball populations ensuring cross-compatibility and that this occurs in the large majority of multigerm seedballs.

The multigerm character found within the genus *Beta* section *Beta* allows the species successfully to colonize new areas, as is evident by the occurrence of isolated populations. While the initial

TABLE 1. RESULTS OF SEEDBALL INVESTIGATIONS IN *BETA VULGARIS*

Seed from collection in Department of Plant Biology, Birmingham University.

Subspecies of *Beta vulgaris*	Source	Description	Mean number of seedlings per seedball	Number of seedball populations setting seed (out of 3)
cicla var. *cicla*	Turkey	Primitive cultivar	2.3	3
" " "	Corfu	Primitive cultivar	2.0	2
cicla var. *flavescens*	U.K.	Commercial cultivar	3.7	3
maritima var. *maritima*	Hungary	North Sea coast type	2.7	3
" " "	Berlin Bot. Gdns	North Sea coast type	4.0	3
vulgaris	Turkey	Local cultivar	2.3	2
"	Turkey	Local cultivar	3.3	3
"	Turkey	Local cultivar	2.7	2
"	Turkey	Local cultivar	2.3	3
"	Turkey	Primitive landrace	3.0	3
"	Turkey	Local cultivar	2.3	3
"	Turkey	Local cultivar	2.7	3
"	Turkey	Primitive landrace	3.0	3
"	Turkey	Primitive landrace	2.3	2
"	Vavilov Inst.	U.S.S.R., cultivar	2.0	3
"	Vavilov Inst.	China, cultivar	2.3	2
"	Vavilov Inst.	U.S.S.R., cultivar	3.3	2
"	Vavilov Inst.	U.S.S.R., cultivar	3.3	3
"	India	Local cultivar	3.7	3
"	Corfu	Local cultivar	2.3	3

population may have a restricted gene pool, in subsequent years and generations this may be enlarged by contact with other populations.

Finally, as noted by Astley & Ford-Lloyd (1981), the staggered flower-opening within the multigerm clusters at the time of pollination should increase the possibility of fertilization by different pollen parents and so widen the genetic base of the individuals within the founder seedball population.

REFERENCES

Astley, D. & Ford-Lloyd, B. V. (1981). The evolutionary significance of multigermicity in the genus *Spinacia* (Chenopodiaceae). *Pl. Syst. Evol.*, **137**: 57–61.

Baker, H. G. (1955). Self-incompatibility and establishment after "long-distance" dispersal. *Evolution, Lancaster, Pa.*, **9**: 347–348.

Baker, H. G. (1965). Characteristics and modes of origin of weeds, in Baker, H. G. & Stebbins, G. L., eds. *The genetics of colonising species*, pp. 147–172. New York.

Barrett, P. H. (1977). *The collected papers of Charles Darwin. I.*, pp. 255–258. Chicago.

Larsen, K. (1977). Self-incompatibility in *Beta vulgaris* L. *Hereditas*, **85**: 227–248.

Stebbins, G. L. (1957). Self-fertilisation and population variability in the higher plants. *Am. Nat.*, **9**: 337–354.

(*Accepted July 1984*)

Short Notes

REDISCOVERY OF THE HERBARIUM OF T. B. FLOWER

Thomas Bruges Flower (1817–1899), who carried out much field-work particularly in Somerset and Wiltshire in the middle years of the last century, formed a valuable herbarium which hardly any of his contemporaries were ever privileged to set eyes on. A conservationist before his time, he preferred not to disclose the localities of rarities that he had discovered and – as White (1912) and Grose (1957) were later led to conclude – was intentionally inaccurate in imparting the details of these to others. Only on the sheets in his herbarium, it has been supposed, were the data entered up correctly; and it has therefore been a matter of intense frustration to subsequent Flora writers that the collection, last reputed to exist in 1937 (Grose 1944), has not been available for study and latterly has appeared to have been lost.

Flower was also an enthusiastic collector of botanical manuscripts and is known to have acquired those of the Bath apothecary William Sole (1741–1802), the author of *Menthae Britannicae*. In 1974 one of us (H.S.T.) started a search for these, which are on record as having passed originally from Sole to his friend, the Rev. Benjamin Richardson, a geologist of Farleigh Hungerford, Somerset (Jenyns 1867: 57). From the Richardson family they subsequently passed in turn to the Flower family, according to Simpson (1960), who cites the W. Bowles Barrett MSS at Weymouth Public Library as his source for this statement. In checking this, a 'Botanical Common Place Book' of Barrett's was also found, on f. 79 of the second volume of which he had noted: "Mr Flower left his herbarium and botanical books to the father of Mr [name left blank]. Mrs Harper believes that his [sic] father intends to present them to the Plymouth Museum 16.4.1908".This added considerably to what Grose (1944) had been able to ascertain.

Enquiries were accordingly made at Plymouth City Museum and Art Gallery and these revealed that a number of sheets of Flower's did indeed exist there (though no trace could be found of any manuscripts of his). Being unaware of the special interest of the Flower herbarium, H.S.T. saw no cause to pass this information on. It was only on the appearance of the note by Dillon (1984) that he realized the herbarium was still being sought. Shortly afterwards the issue of the prospectus for Kent & Allen (1984) put the two of us in touch on the matter. Although all museums in the British Isles had been circularized with a request for details of the herbaria in their possession in connection with the latter publication, no report of any Flower sheets had been received. By an equal mischance, the note by Dillon had been overlooked at Plymouth Museum. It was the converging of our respective searches that thus proved crucial.

Subsequent enquiries by D.E.A. have established that the sheets in question total nearly two thousand and are thus likely to constitute Flower's actual herbarium (or at any rate what remains of it) rather than some subsidiary collection or a mere set of duplicates. Unfortunately the Museum records reveal no more than that the collection was accessioned in 1939. It is evident that it could have been donated by the Harper family to Plymouth Museum at any time between 1915, when Dr Harper died, and 1939.

Meanwhile the Sole – Richardson – Flower manuscripts remain untraced. Any information which may help in locating them would be most welcome.

ACKNOWLEDGMENTS

We are indebted to Mr D. A. Curry, Keeper of Natural History at Plymouth City Museum and Art Gallery, for arduously combing the Museum's herbarium for Flower sheets and for providing some of the information in this note. The staff at Weymouth Central Reference Library were equally helpful.

REFERENCES

Dillon, P. J. (1984). The enigmatic Thomas Bruges Flower (1817–1899): a challenge for modern collections research? *South West nat. Sci. Colls. Res. Unit Newsletter*, **1** (2): 37–39.

Grose, J. D. (1944). Note, in *Rep. botl Soc. Exch. Club Br. Isl.*, **12**: 465.

Grose, J. D. (1957). *The flora of Wiltshire*, p. 38. Devizes.

Jenyns, L. (1867). Lecture on the Bath flora. *Proc. Bath nat. Hist. Antiq. Field Club*, **1**: 25–63.

Kent, D. H. & Allen, D. E. (1984). *British and Irish herbaria*. London.

Simpson, N. D. (1960). *A bibliographical index of the British flora*, p. 120. Bournemouth.

White, J. W. (1912). *The Bristol flora*, p. 90. Bristol.

D. E. Allen
Lesney Cottage, Middle Road, Winchester, SO22 5EJ
H. S. Torrens,
Geology Department, Keel University, ST5 5BG

CHROMOSOME NUMBERS OF SOME ALIEN *REYNOUTRIA* SPECIES IN THE BRITISH ISLES

Reynoutria sachalinensis (F. Schmidt Petrop.) Nakai 2n=44.
V.c. 17, Surrey: Elmbeamswood, Elstead, GR 41/89.41
V.c. 43, Rads.: Howey, GR 32/051.587
V.c. 48, Merioneth: Brithdir, Caernywch Hall (garden), GR 23/761.177
V.c. 51, Flints.: Nant Y Frith, Bwlchgwyn, GR 32/265.542
V.c. H.16, W. Galway: Ballyconneely, Connemara, GR 02/620.446; Errislannan, Clifden, GR 02/620.495

Reynoutria japonica Houtt. var. *compacta* (J. D. Hook.) Buchheim 2n=44.
V.c. 16, W. Kent: Platt (garden), GR 51/616.572
V.c. 55, Leics.: Broughton Astley (garden), GR 42/525.927

Reynoutria japonica Houtt. var. *japonica* 2n=88.
V.c. 2, E. Cornwall: Liskeard, GR 20/188.643; St Austell, GR 20/052.532 (c. 88)
V.c. 11, S. Hants.: Petersfield, GR 41/744.234; Stroud, Petersfield, GR 41/720.234
V.c. 12, N. Hants.: Heckfield, Hook, GR 41/726.612; Itchen Abbas, GR 41/541.329
V.c. 17, Surrey: Hindhead, GR 41/886.356; Chilworth – Shalford, GR 51/012.466
V.c. 44, Carms.: Ammanford, GR 22/61.11
V.c. 46, Cards.: Aberystwyth, GR 22/601.820
V.c. 48, Merioneth: Dolgellau, GR 23/711.823; Tyn Coed, GR 23/67.18; Brithdir, Caerynwch Hall (garden), GR 23/761.177; Boston Lodge, Minfford, GR 23/589.382; Llanfihangel-y-Traethau, GR 23/597.353
V.c. 49, Caerns.: Pentre'r-felin, GR 23/526.396; Pwllheli, GR 23/374.350; Criccieth, GR 23/492.381; Llangwnadl, GR 23/218.335
V.c. 55, Leics.: Knighton, GR 43/617.013; University Botanic Garden, Leicester, GR 43/617.015; Sileby, GR 43/602.153; Stoughton, GR 43/644.026; Dunton Basset, GR 42/549.892

Reynoutria tetraploids 2n=44.
V.c. 17, Surrey: Gomshall Station, GR 51/09.48
V.c. 33, E. Gloucs.: Cirencester (plant no. 1), GR 41/039.033
V.c. 66, Co. Durham: South Wylam, GR 45/124.646

Reynoutria hexaploids 2n=66.
V.c. 14, E. Sussex: Lye Green, GR 51/511.336 (c. 66)
V.c. 33, E. Gloucs.: Cirencester (plant no. 2), GR 41/039.033 (c. 66)

V.c. 48, Merioneth: Dolgellau, GR 23/711.823; Brithdir, Caerynwch Hall (garden), GR 23/763.177; Pont Rhyd Sarn, near. Bala, GR 23/859.287
V.c. 55, Leics.: Loughborough, GR 43/544.204
V.c. 60, W. Lancs.: Preston, GR 42/510.298 (c. 66)
V.c. H.16, W. Galway: Maam, GR 02/963.533; Roundstone, GR 02/726.424

The rhizomatous perennials, *Reynoutria japonica* (*Polygonum cuspidatum* Siebold & Zucc.) and *Reynoutria sachalinensis* (*Polygonum sachalinense* F. Schmidt Petrop.), introduced to the British Isles last century are now firmly established with a well-earned reputation as invasive and persistant weeds (Conolly 1977). Characteristics which allow *R. japonica* to be an early colonist of lava fields in Japan ensure that it is well able to cope with habitats ranging from urban waste land to Welsh hillsides.

The threat posed by *R. japonica* is now recognized in law since it is one of the land plants which it is illegal to introduce into the wild in Britain. It was against this background that we set out to learn more about the mode of spread and reproductive biology of these plants. Since published work (none of it carried out on British plants) revealed counts of 2n=44, more than 60, and 88 for *R. japonica* var. *japonica*, 2n=44 for *R. japonica* var. *compacta*, and 2n=44, c. 66 and 102 for *R. sachalinensis* (Federov 1969; Moore 1973, 1977), we made an examination of the chromosome numbers of British and Irish plants our starting point.

On the basis of evidence to be presented in a later paper, it appears that the base chromosome number for *Reynoutria* is 11. Our results show that three different ploidy levels are present in Britain. All *R. sachalinensis* and *R. japonica* var. *compacta* plants examined so far are represented only at the tetraploid level. *R. japonica* var. *japonica*, on the other hand, is found to be octoploid at the 24 sites in the survey. The octoploid *R. japonica* is the most usually encountered and the 24 locations were taken on an arbitrary basis. The nine hexaploid plants, however, were collected because they differed in some way from the plants usually encountered, and morphologically and cytologically suggest a possible hybrid origin. The Brithdir specimen (2n=66) is almost certainly a hybrid between *R. japonica* (2n=88) and *R. sachalinensis* (2n=44) and the plants at Preston and Pont Ryhd Sarn may well be of the same origin. Three tetraploid plants were also found and, although superficially similar to *R. japonica*, there are signs that these too may be interspecific hybrids. The clone at South Wylam (2n=44) may be of hybrid origin at the tetraploid level. Work is now in progress in comparing these plants morphologically and cytologically with plants produced by controlled pollinations between the two species, and between ploidy levels within *R. japonica*.

All voucher specimens are in **LTR**.

ACKNOWLEDGMENTS

We would like to thank Dr C. A. Stace for his encouragement and Mrs E. Neale for her horticultural skills.

REFERENCES

Conolly, A. P. (1977). The distribution and history in the British Isles of some alien species of *Polygonum* and *Reynoutria*. *Watsonia*, **11**: 291–311.
Fedorov, A. A. (1969). *Chromosome numbers of flowering plants*. Leningrad.
Moore, R. J., ed. (1973). *Index to plant chromosome numbers. 1967–1971*. Utrecht.
Moore, R. J., ed. (1977). *Index to plant chromosome numbers for 1973–74*. Utrecht.

J. P. Bailey & A. P. Conolly
Botany Department, The University, Leicester, LE1 7RH

VARIATION IN THE FLORAL MORPHOLOGY OF *LINARIA REPENS* (L.) MILL.

In September 1979, *Linaria* plants were seen on a slag-heap adjacent to a disused quarry near Cathkin, Lanarkshire, v.c. 77 (GR 26/621.583). While the corolla colour and seed morphology were typical of *L. repens* (L.) Mill. the flower dimensions suggested to different individuals the possibility of hybridization with either *L. vulgaris* Mill. (*L.* × *sepium* Allman) or *L. purpurea* (L.) Mill. (*L.* × *dominii* Druce).

We revisited the site in September 1981 to look for evidence of hybridization and again in September 1983 to measure further fresh material in order to obtain corolla length/spur length against corolla height/spur length ratios.

In September 1981 we estimated that in an area 30 × 15 m there were approximately 2,000 plants. All the flowers were identical in colour, being basically white with many violet veins on the corolla and standards, but only a few on the lower lips. There were orange hairs on the palate and in a line from there extending proximally on each side of the midline. Capsule formation was almost 100% and every capsule opened contained seeds.

20 flowers were selected at random from each end of the site and from the middle. Spur lengths of these flowers averaged 4.3, 4.3 and 4.4 mm (range 3–5 mm). As the results from each section were so similar, no further distinction was made while making subsequent measurements. The length from pedicel apex to the point at which the corolla split into upper and lower lip was, on average, 3.8 mm (range 3–4 mm); and the corolla length from pedicel apex to the tip of the boss of the lower lip averaged 8 mm (range 7–9 mm). From measurements made in 1983, the average corolla length/spur length was found to be 1.9 and the corolla height/spur length 2.2. The plants were rhizomatous.

Although the corolla length/spur length and corolla height/spur length ratios are intermediate between those of *L. purpurea* and *L. repens* (Stace 1982), the light corolla colour and creeping rootstock rule out *L. purpurea* × *repens* (Stace 1975). Indeed, the nearest population of *L. purpurea* occurs in a Glasgow park, 5.5 km to the north of the Cathkin site. In *L. repens* × *vulgaris* the corolla is yellowish; furthermore the hybrid is highly fertile and backcrosses readily (Stace 1975). Our results indicate that the large population of 2,000 more or less identical plants is not a variable hybrid swarm but a constant population of a taxon. We consider the plants to be an extreme form of *L. repens*.

Warburg (1962) and Rose (1981) stated that in *L. repens* the spur is short and straight and about a quarter as long as the rest of the corolla. Rose (1981) gives an illustration of comparable dimensions (spur 3 mm; rest of corolla 10 mm).

We have seen specimens of *L. repens* from other sites, and obtained from a colleague garden material with dimensions which agree with those quoted above, but the Cathkin plants have average spur lengths of 4.3 mm and corollas of 8 mm.

These measurements actually agree with illustrations in Ross-Craig (1966) and Butcher (1961) and suggest that the published descriptions should be changed to take account of the fact that the spur may be half as long as the rest of the corolla. Further, we have noticed that, although short spurs are always straight, those exceeding 4 mm in length are always curved.

ACKNOWLEDGMENTS

We are grateful to Dr C. A. Stace for help with plant identification and to Dr E. Teasdale for supplying garden material.

REFERENCES

Butcher, R. W. (1961). *A new illustrated British Flora*, **2**: 223. London.

Rose, F. (1981). *The wild flower key*, p. 300. London.

Ross-Craig, S. (1966). *Drawings of British plants*, **23**: 10. London.

Stace, C. A. (1975). *Linaria*, in Stace, C. A., ed. *Hybridization and the flora of the British Isles*, pp. 366–367. London.

Stace, C. A. (1982). Segregation in the natural hybrid *Linaria purpurea* (L.) Mill. × *L. repens* (L.) Mill. *Watsonia*, **14**: 53–57.

Warburg, E. F. (1962). *Linaria*, in Clapham, A. R., Tutin, T. G. & Warburg, E. F. *Flora of the British Isles*, 2nd ed., pp. 678–680. Cambridge.

P. & B. C. M. Macpherson
15 Lubnaig Road, Newlands, Glasgow, G43 2RY

BELLIS PERENNIS L. VAR. *DISCOIDEA* HUS

I recently published the name *Bellis perennis* L. forma *discoidea* for variants of our common Daisy that lack ray florets (McClintock 1984). I wrote that I had failed to find any published appellation for this form. Trust Dr Heino Heine to find something! He informs me that Hus (1911) described an aberration which had appeared among a bed of "*delicata*" daisies at the Missouri Botanical Garden: "In the capitula of this specimen the rayflowers had either disappeared or, what is more probable, had been replaced by disc-flowers. The result was a rather striking maroon-red button". He also recorded that André (1909) had mentioned the variety *discoidea* under the name "Paquerette vivace var. double à fleurs tuyautées". In fact, André does not use the word *discoidea*, but Hus (1911) also published a photograph (Fig. 2, p. 648) of "*Bellis perennis discoidea*", and this, together with his name and the diagnosis quoted from André, effectively publish this name at varietal level.

Thus, for those who consider this aberration to be of varietal rank the ascription must be to Hus; those who rate it merely as a form must ascribe it to me, until such time as another keen-eyed lynx discovers an earlier publication, which would not surprise me.

REFERENCES

André, E. (1909). In Vilmorin, P. L. F. L. *Les fleurs de pleine terre*, 5th ed., p. 781. Paris.
Hus, H. (1911). The origin of the species in nature. *Am. Nat.*, **45**: 648–649.
McClintock, D. (1984). Discoid daisies. *Watsonia*, **15**: 119.

D. McClintock
Bracken Hill, Platt, Kent, TN15 8JH

NOMENCLATURAL NOTES ON SOME WILLOW HYBRIDS

The publication of a B.S.B.I. handbook on willows and poplars (Meikle 1984) calls for a few minor nomenclatural innovations, and it is felt that these are better published separately, rather than as an appendix to the book. In most instances the names have already appeared in the botanical or horticultural literature, but without being given the formal validation required under the International Code.

1. **Salix** × **rubens** Schrank nothovar. **basfordiana** (Scaling ex S. J. Salter) Meikle, **comb. nov**.
Basionym: *S. basfordiana* Scaling ex S. J. Salter in *Gard. Chron.*, n. s., **17**: 298 (March 1882).
Synonym: *S. fragilis* L. var. *basfordiana* (Scaling ex S. J. Salter) Bean, *Trees & shrubs hardy in the British Isles*, **2**: 481 (1914).
S. alba L. var. *vitellina* (L.) Stokes × *S. fragilis* L.

Two distinct forms of this nothovariety, both locally frequent in Great Britain and Ireland as cultivated and spontaneous plants, were confused by Salter when he first described the willow hybrid distributed as *S. basfordiana* nom. nud. by the willow-grower William Scaling around 1870. The male plant figured in the *Gardeners' Chronicle* (fig. 42), is unquestionably Scaling's *S. basfordiana*, with long, attenuate leaves, and elongate, ultimately pendulous catkins; it is here distinguished as:

1a. **S.** × **rubens** Schrank nothovar. **basfordiana** (Scaling ex S. J. Salter) Meikle forma **basfordiana** (Scaling ex S. J. Salter) Meikle, **forma nov**.
Ramulis aurantiacis vel testaceis, foliis anguste lanceolatis, longe acuminatis, usque 15 cm longis, 2 cm latis, mox glaberrimis; amentis (masculinis et foemineis) elongatis, anguste cylindricis, 7–8 cm longis (vel interdum longioribus) patentibus tandem pendulis.
HOLOTYPUS: *S. basfordiana* Scaling ex S. J. Salter pro parte quoad plantam masculam solum, *Gard. Chron.*, n. s., **17**: 299, fig. 42 (1882).

Although male and female plants of typical *S.* × *rubens* nothovar. *basfordiana* are equally frequent, the female plant figured by Salter (1882) is a distinct taxon, originally distributed by Scaling as "*Salix sanguinea*", and included in Bean (1980) under the cultivar name *Salix*

'Sanguinea'. I am not aware that the name has ever been formally validated at any rank, and here propose:

1b. **Salix × rubens** Schrank nothovar. **basfordiana** (Scaling ex. S. J. Salter) Meikle forma **sanguinea** Meikle, **forma nov**.

A forma *basfordiana* differt ramulis rubris (nec aurantiacis), foliis brevioribus, raro 8 cm excedentibus, amentis foeminis brevioribus, 3–4 cm longis, maturitate patentibus vel suberectis, eisdem masculis ignotis.

HOLOTYPUS: Great Britain, Middlesex, side of the R. Thames opposite Mortlake brewery, 20 April [and 14 Sept.] 1949, *Meikle 1571* (**K**).

2. **Salix × sepulcralis** Simonk. nothovar. **chrysocoma** (Dode) Meikle, **comb. et stat. nov.**

Basionym: *S. chrysocoma* Dode in *Bull. Soc. bot. Fr.*, **55**: 655 (1909).

S. alba L. var. *vitellina* (L.) Stokes × *S. babylonica* L.

The most popular of the 'Weeping Willows', with very pendulous, yellow twigs, very commonly cultivated in gardens. Although common as an ornamental, I have no evidence that it has been given a formal name as a variety (or nothovariety) of the hybrid *S. alba* L. × *S. babylonica* L. (*S.* × *sepulcralis* Simonk.). Its origin is obscure, but there can be little doubt that it is *S. alba* var. *vitellina* × *S. babylonica*, and not just a pendulous variant of *S. alba* var. *vitellina*, as some authors have suggested.

3. **S. × pendulina** Wenderoth var. **elegantissima** (K. Koch) Meikle, **comb. et stat. nov.**

Basionym: *S. elegantissima* K. Koch in *Wschr. Ver. Beförd. Gartenb. Preuss.*, **14**: 380 (1871).

This rather rarely cultivated plant appears to be one of several variants of the hybrid *S. babylonica* L. × *S. fragilis* L., for which I adopt the earlier name *S.* × *pendulina* Wenderoth in preference to the more familiar, but later, *S.* × *blanda* Anderss.

4. **Salix × grahamii** Borrer ex Baker var. **moorei** (F. B. White) Meikle, **comb. et stat. nov.**

Basionym: **S. × moorei** F. B. White in *J. Linn. Soc., Bot.*, **27**: 438 (1890).

S. × *moorei* F. B. White differs from *S.* × *grahamii* Borrer ex Baker only in having rather longer, narrower catkin-scales, thinly, occasionally rather densely, pilose ovaries, and glabrous pedicels. It must without doubt have the same parentage as *S.* × *grahamii*, of which it can be considered no more than a variety.

REFERENCES

BEAN, W. J. (1980). *Trees and shrubs hardy in the British Isles*, 8th ed., **4**: 273. London.

MEIKLE, R. D. (1984). *Willows and poplars of the British Isles*. London.

SALTER, S. J. (1882). *Salix basfordiana*. *Gard. Chron.*, n. s., **17**: 298, fig. 41.

R. D. MEIKLE
Ranscombe Lodge, Wootton Courtenay, Minehead, Somerset, TA24 8RA

RUPPIA SPIRALIS L. EX DUMORT. IN YORKSHIRE

The recent discovery of *Ruppia spiralis* L. ex Dumort. at Kilnsea, S.E. Yorks., v.c. 61, has been documented by Crackles (1983). Because of taxonomic and, more particularly, nomenclatural confusion between *R. spiralis* (*R. cirrhosa* (Petagna) Grande, *R. maritima* auct.) and *R. maritima* L. (*R. rostellata* Koch), early *Ruppia* records are often difficult to interpret unless they are substantiated by herbarium specimens. Although the first published record of *Ruppia* in S.E. Yorks. is of *R. spiralis* (Robinson 1900), this was subsequently reported by Robinson (1902) as *R. rostellata*. In the absence of any herbarium specimen, Miss Crackles concluded that the recent discovery was the first certain record of *R. spiralis* in Yorkshire and the first record on the eastern coast of Britain north of the Humber.

I recently had occasion to look at *Ruppia* specimens in **BM**, and found there three sheets of *R. spiralis* collected in Yorkshire. These specimens not only show that there are earlier records of *R. spiralis* in v.c. 61, but also extend its northern limit on the east coast. The details of the specimens are as follows:

a) Brackish pools on salt-marsh near Salt End, Hedon, v.c. 61, GR 54/16.27., 2 September 1907, *C. Waterfall.*

b) Dyke near Long Bank, near Kilnsea, v.c. 61, GR 54/4..1.., 13 June 1933, *W. A. Sledge*, det. J. E. Dandy. (There are also specimens of this gathering in **CMM** and **RNG**).

c) Coatham, v.c. 62, GR 45/5..2.., August 1852, *J. G. Baker*, det. J. E. Dandy.

The sheet from Hedon does not bear a det. slip of Dandy's, probably because it is the only one of the three specimens actually labelled *R. spiralis.* The specimen has sinuous peduncles 7–10 cm long, which confirm the identity of the plant. Dr N. T. H. Holmes has kindly examined all three specimens at **BM** and agrees that they are *R. spiralis.*

The specimens collected in 1933 substantiate the published record of *R. spiralis* (as *R. maritima*, the name then applied to *R. spiralis*) from Kilnsea (Sledge 1934; Lees 1941). They suggest the possibility that the species may have persisted in the Kilnsea area (but not in the recently discovered site, a pit excavated in 1978–1979) from 1933 until its rediscovery in 1981. It perhaps evaded detection for so long if, as Crackles (1983) suggests, it either does not fruit or fruits late in the season at the northern edge of its range.

In addition to the record from Coatham, N.E. Yorks., *Ruppia spiralis* has been recorded from the Durham side of the River Tees. In 1917 J. W. Heslop Harrison found *R. spiralis* growing in small quantity with masses of *R. maritima* in pools in Greenabella Marsh, v.c. 66, GR 45/5.2. (G. G. Graham, in litt. 1983). This is apparently the northernmost record of *R. spiralis* on the east coast, although there are reliable records of the species from the Outer Hebrides, Orkney and Shetland (Perring & Walters 1976).

ACKNOWLEDGMENTS

I am grateful to Miss Crackles, Mr Graham and Dr Sledge for help in writing this note.

REFERENCES

Crackles, F. E. (1983). *Ruppia spiralis* L. ex Dumort. and *R. maritima* L. in S.E. Yorkshire. *Watsonia*, **14**: 274–275.

Lees, F. A. (1941). *Ruppia maritima* L., in Cheetham, C. A. & Sledge, W. A., eds. *A supplement to the Yorkshire Floras*, p. 111.

Perring, F. H. & Walters, S. M., eds (1976). *Atlas of the British flora*, 2nd ed., p. 310. London.

Robinson, J. F. (1900). East Riding botanical notes, 1900. *Trans. Hull scient. Fld Nat. Club*, **1**: 117.

Robinson, J. F. (1902). *The flora of the East Riding of Yorkshire*, p. 196. London.

Sledge, W. A. (1934). The Yorkshire Naturalists' Union's seventy-second annual report, for 1933. Flowering plants. *Naturalist, Hull*, **1934**: 43–45.

C. D. Preston
Institute of Terrestrial Ecology, Monks Wood Experimental Station, Abbots Ripton, Huntingdon, PE17 2LS

SOME UNUSUAL ORCHID VARIANTS FROM ANGLESEY

Individuals with white flowers occur occasionally in a number of our wild orchid species, but the frequency with which they do so varies considerably from one species to another. Albino plants of *Orchis morio* L. have been found on a number of occasions in Anglesey over the last 30 years, but white-flowered plants of *O. mascula* (L.) L. turn up far less frequently, even though this species is much the commoner of the two. Consequently when one was seen in Cors Goch Nature Reserve in the spring of 1983, it attracted a good deal of attention, especially from photographers.

This plant was found at the foot of the limestone scarp which runs along the south-eastern edge of the fen. It was a fairly robust specimen, over 27 cm tall, with a large spike of white flowers, but closer examination showed that the purple spots which normally occur in the central area of the labellum were present, though much fainter than usual. In this plant, too, the deep coloration, normally found on the upper part of the stem and on the bracts and the ovaries, was absent, and the leaves appeared to lack any kind of spotting. This agrees with observations elsewhere that white-flowered plants of this species mostly have unspotted leaves, although exceptions to this have been recorded, according to Summerhayes (1951).

A few weeks later, during a visit to Cors Erddreiniog N.N.R., the warden, Mr L. T. Colley, showed me a white-flowered plant of *Dactylorhiza traunsteineri* (Sauter) Soó. In this the flowers were a pure white with no trace of colouring at all, even in the form of faint marks on the labellum. In all other respects the flowers were typical of this species, the labellum having the usual deltoid shape, shallowly tri-lobed with the mid-lobe projecting and the lateral lobes moderately reflexed. There were only 6 or 7 flowers in the spike, which was rather loose and secund, but the bracts and the upper part of the stem were green and lacked the deep reddish-purple colour normally found in this species. Otherwise the plant was quite typical, having a rather slender, flexuous stem about 17–20 cm tall and carrying four narrow leaves.

Albino plants are very rare in *D. traunsteineri*. The only other record of one from Britain is from Yorkshire, where it was found by Mr D. J. Tennant a few years ago. This situation contrasts with that in *D. incarnata* (L.) Soó in which albino plants are found much more frequently: they can often be seen at some Anglesey localities where they are sometimes mistaken for subsp. *ochroleuca* (Boll) P. F. Hunt & Summerhayes.

The third unusual plant, one of *Ophrys insectifera* L., was also found by Mr Colley a year previously, in 1982, at another fen area known as Cors Bodeilio. This place is two miles south-west of Pentraeth and *O. insectifera* was recorded here as long ago as 1813 by Hugh Davies. The species occurs here regularly and sometimes in good numbers: over 60 plants were counted in flower in June 1981. The abnormal specimen found by Mr Colley had two labella, four sepals instead of three, a third narrow, brown petal like those forming the antennae of the "fly", and two stamens. All the flowers which had opened were identical and were also peculiar in that the labella had two sinuses at the apex instead of one and were held almost horizontally and not more or less vertically as in normal flowers. The sketch of a flower of the Cors Bodeilio plant (Fig. 1) was made from a photograph taken by Mr Colley. Summerhayes (1951) has described another mutant form of *O. insectifera* in which the two "antennae" were replaced by additional labella so that there were three "bodies" to the fly.

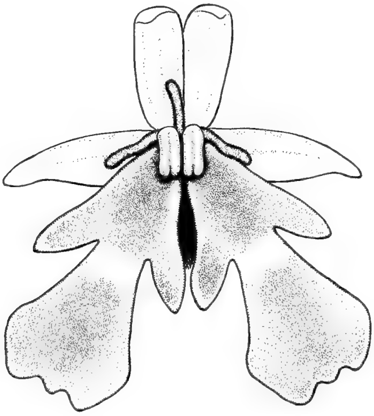


FIGURE 1. Single flower of mutant *Ophrys insectifera*. Scale bar = 1 mm.

Yet another uncommon orchid variety came to light when Mr M. Hammett showed me some photographs of orchids taken in various localities in Anglesey in June 1983. Among them was a mutant *Ophrys apifera* Hudson which proved to be the very distinct var. *bicolor* (Naegeli) Nelson. In this the lip completely lacked the usual pattern of lines and blotches, and the basal part, where the speculum is normally found, was a pale greenish-brown, shading to a dark chestnut-brown at the apex. This variety is beautifully illustrated by Danesch & Danesch (1968: Abb. 159) and by Davies *et al.* (1983: photo 316). Mr Hammett's photograph shows a plant with flowers identical with these illustrations. It had been found among the sand-dunes near Rhosneigr and there appears to be no previous record of this variety from the island.

REFERENCES

Davies, H. (1813). *Welsh Botanology*. London.
Davies, P., Davies, J. & Huxley, A. (1983). *Wild Orchids of Britain and Europe*. London.
Danesch, O. & Danesch, E. (1962). *Orchideen Europas, Mitteleuropa*. Berne & Stuttgart.
Summerhayes, V. S. (1951). *Wild Orchids of Britain*. London.

R. H. Roberts
51 Belmont Road, Bangor, Gwynedd, LL57 2HY

OROBANCHE CARYOPHYLLACEA SM. IN NORTH WALES

During the course of an investigation into the genus *Orobanche* in Britain (Rumsey 1984), I came across two specimens of *O. caryophyllacea* Sm. (Clove-scented Broomrape) from North Wales. This plant is widely accepted to be restricted to a small area in East Kent, v.c. 15, and until now the only other records have been from Suffolk (Simpson 1982) (certainly in error for *O. rapum-genistae* Thuill.) and Argyll. This latter record is based on an 1844 specimen, which was originally determined as *O. elatior* Sutton, from the Loch Nell area. The specimen is at **K** and has been correctly redetermined as *O. caryophyllacea*.

Given the plant's accepted range in Britain, I treated the first Welsh specimen (Conway Castle, v.c. 49, August 1883, *J. W. Reed* (**RNG**)) that I found with scepticism. Originally determined as *O. hederae* Duby., the sheet indeed consists partly of that species but also partly of *O. caryophyllacea*. I assumed that some error had occurred during the preparation of the sheet, and that *O. caryophyllacea* from another locality had been mixed mistakenly with Welsh *O. hederae*; Reed's herbarium does contain much European material. However, there is a second mixed sheet of *O. caryophyllacea* and *O. hederae* from the same locality (July 1890, *S. H. Bickham* (**CGE**)), also labelled *O. hederae*. Even given that the *O. caryophyllacea* plants are smaller than usual, it is difficult to see how two botanists could independently mix foreign material with *O. hederae* from Conway Castle. I therefore believe that *O. caryophyllacea* could have existed in this botanically rich area in the last quarter of the nineteenth century and provisionally suggest that the species be accepted as a native Welsh plant. I hope that searches both in this area and at Loch Nell, Argyll, will prove me right and thereby gain us sites for a very rare and beautiful plant.

REFERENCES

Rumsey, F. J. (1984). *A consideration of the status of the family Orobanchaceae*. B.Sc. thesis, Reading University.
Simpson, F. W. (1982). *Simpson's Flora of Suffolk*, p. 305. Ipswich.

F. J. Rumsey
Botany Department, The University, Whiteknights, Reading, RG6 2AS

Book Reviews

Atlas Florae Europaeae. Volume **6**, *Caryophyllaceae (Alsinoideae and Paronychioideae)*. Edited by J. Jalas & J. Suominen. Pp. 176. Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo. 1983. Price £44.00 (ISBN 951–9108–05–X).

The sixth volume of this *Atlas* series is, like its predecessors, a welcome addition to the European floristic literature. The systematic arrangement follows that of *Flora Europaea*, but accommodates a number of changes in taxonomy, nomenclature and geographical distribution. The editors, who should be warmly encouraged in their long task, have now reached over a third of the way through the first volume (1964) of *Flora Europaea*; and, when a subsequent volume has treated the subfamily Silenoideae of Caryophyllaceae, they will have passed the magic half-way mark in Volume 1!

As in the earlier volumes of the *Atlas*, the distribution of individual species is displayed on the basis of the UTM 50-km-square grid. Symbols depicting native, adventive, dubious, unknown or extinct status readily conceptualize distribution patterns and provide the reader with images to compare those of different species. In many cases, useful notes are provided that point out areas where problems exist (taxonomic controversy, under-recording, etc.) and frequently emphasize, as did *Flora Europaea*, the need for further research. Full synonymy is given, also information on other published maps that give the total range of a species. At the same time, the *Atlas* includes valuable amendments to *Flora Europaea*, notably including data assimilated post-1964 on species and subspecies that have been described as new to science from Europe, species newly found to occur in Europe (but already known elsewhere in the world), and adventives regarded as having become naturalized in Europe during the last 20 years. Some of this material has not perhaps received enough critical evaluation, in view of the broad, 'overall' species concept that was favoured by the editors of *Flora Europaea*. Although *Flora* and *Atlas* are distinct projects, it can be no bad thing for them to tally as much as possible. It is therefore fortunate that *Flora Europaea* Volume 1 is currently being revised at Reading University, thus allowing an excellent opportunity for close cooperation between these two projects, especially with regard to matters such as taxonomic rank.

This volume of the *Atlas* is particularly meaty, containing as it does the many critical and obscure taxa of such genera as *Arenaria*, *Cerastium*, *Minuartia* and *Paronychia*, each with a great range of local endemics and widespread species. The maps give the British and Irish reader a broad picture of our own flora, so much of which represents marginal fragments of a wider European distribution. The maps of, for example, *Minuartia verna* subsp. *verna* and *Scleranthus perennis* are good illustrations of this. Such patterns make these *Atlas* volumes compulsive browsing – they can hardly be described as 'a good read' – for both the involved research worker and the armchair botanist. The high price will deter most purchasers, although the excellent quality of the paper, printing and layout makes this an attractive series for the bibliophile. I look forward to subsequent volumes of this splendid publication, which at the present rate of progress should appear at about two-yearly intervals.

J. R. AKEROYD

Wild flowers in their habitats. Desmond & Marjorie Parish. Pp viii+168 with 95 colour plates. Blandford Press, Dorset. 1984. Price (paperback) £3.95 (ISBN 0–7137–1395–X).
Flowers in the wild. Marjorie & Desmond Parish. Pp 160 with 446 colour plates. Blandford Press, Dorset. 1983. Price £8.95 (ISBN 0–7137–1178–7).

To many of us, wild plant pictures have a compulsive appeal; and these two books of coloured photographs by the experienced plant photographers Mr and Mrs Parish will reward anyone drawn by the promise of their titles.

Wild flowers in their habitats (originally published in hardback as *Wild flowers – a photographic guide*, 1979) is now a compact 19.5 × 14.5 cm paperback with 95 full- or half-page plant portraits. My favourite plant photographs are those showing the growing plant in natural setting (and this is surely where a photograph most usefully contributes to and complements a botanical drawing?) – so it was disappointing in view of the new title to find that 23 of these are flower close-ups, some taken with flash showing them against a black, dark or unnaturally thundery background, giving a splendid *flower* picture but no indication of the habitat or plant associations. The habitats are however described in the text and the plants grouped in a sequence of nine habitats, as indicated in the contents list. The plants portrayed range in distribution from the Arctic Circle to the Mediterranean shores, and from the Atlantic Coast to the borders of Asia. The selection from such a diverse area must include the authors' personal favourite photographs, and these are offered as a "small sample of the plant kingdom". About half are found in Britain; distribution notes on each chosen species are given in the text, together with a plant description and notes on points of interest. A plea for conservation in the Introduction is supplemented by further references in the texts on rarer species; for example, of *Lloydia serotina* the authors say "the world distribution justifies the need for especial care for small colonies" (as in Britain) "which have their place in the fascinating uncompleted jig-saw of worldwide ecology".

Flowers in the wild is similarly described as a wide selection of photographs of British and European wild flowers, but with the much larger number of 446 species included. Again the plants are grouped under habitats, this time seven, and under habitat headings. With seven photographs on each double page, arranged around a column of text – a format familiar in a series of European alpine flower books – each section makes a 'picture-book' of some of the wild plants of those habitats, which are more fully described in ten pages of Introduction. There is also finally a page on conservation and on the photography. Both books include a glossary, a bibliography, and separate English and Latin indices of plant names.

These two books can be seen as the product of a lifetime's partnership in photographing flowers, with the authors' enjoyment evident. Many of the pictures are evocative. The authors hope that through the photographs others may revive "personal and joyous experience"; they should indeed enable those fortunate in having travelled in search of flowers to relive happy plant-hunting moments and encourage others to follow in their footsteps.

M. BRIGGS

Flowering plants of Wales. R. G. Ellis. Pp. ix+338, with coloured frontispiece, 1028 distribution maps and an overlay. Amgueddfa Genedlaethol Cymru/National Museum of Wales, Caerdydd/Cardiff. 1983. Price £12.00 (ISBN 0–7200–0271–0).

This superbly produced volume is no mere third edition of its predecessor, Hyde & Wade's *Welsh flowering plants* (1934, 1957), which was basically an enumeration of the specimens and records at Cardiff, but is a wholly new production incorporating records up to the end of 1981 from a wide range of information sources. It not only catalogues all taxa of flowering plants down to the rank of subspecies (though not varieties) that have been recorded "apparently growing wild in Wales", but maps, on the 10-km-square basis, the Welsh distribution of the majority. There are 1521 species, 325 microspecies (*Rubus*, *Taraxacum*, *Hieracium*) and 282 hybrids, with conspicuous planted forest trees for good measure. A valuable source of information is given by the inclusion of all taxa not obviously planted: 653 casuals, many from Glamorgan, and over 400 aliens and introductions.

The sequence in the Catalogue follows *Flora Europaea*, as does the nomenclature, in the main. Entries give the usual data on names (including Welsh ones), status, month of flowering, frequency, v.c. and 10-km-square distribution, and habitat synopses; these occasionally appear more pertinent to south Wales than to the north-west. The geographical element assignations must be sought in the index not the text; some are original. Abbreviations used here and elsewhere, symbols, details of arrangement and plan are all carefully indicated, though variously located. The references, intentionally not a bibliography, are tantalizingly brief; many are merely "pers. comm.".

Preliminary sections cover notes on the National Museum of Wales Herbarium (**NMW**), a short history of botanical recording in Wales, and vice-county botanical highlights. Special chapters on 'The geological background' (Owens & Bevins) and on 'The effect of climate past and present on plant distribution in Wales' (Savidge) will be much appreciated, the latter accompanied by a stimulating, coloured, bioclimatic map forming the book's frontispiece.

Errors are impressively hard to find: "Llangain" (p. 109) should read "Llangian"; "*Festuca guestfalica*" (p. 172) ought to be "*F. longifolia* Thuill."; "*Polygonum lichiangense*" (p. 49) I suspect to be an error for *P. polystachyum*; superscript reference to *Ulmus plotii* × *procera* (p. 47) is not 77 but 74. On p. 85, the entry for *Potentilla anglica* × *reptans* would have been better under *P.* × *mixta*, for which the two possible origins (Stace 1975) include also *P. erecta* × *reptans*. Similarity between these *two* hybrids implies the unlikelihood that the actual parentage was known for all the entries mapped.

Ubiquitous species, recorded from at least 251 of the 282 Welsh 10 km squares, have the 'missing' squares listed; the rarest taxa have full details for every locality (sometimes disguised); those with 10-19 squares have these listed. Species with 20–250 squares are mapped. Here lies my only criticism, and a major disappointment: the sad decision whereby the map symbols merely distinguish 'pre-1930' from 'post-1930' entries. This decision was made despite the extensive updating of *Atlas* 1950+ records, the data for which are held at NMW. So, though many entries will be recent, assumption of even a post-1950 date cannot, alas, be made. A caution is necessary regarding the 'introduced' symbol, which is used only where the relevant taxon is native *somewhere* in Wales; taxa deemed not native anywhere in the Principality have the same symbols as the natives. A transparent overlay in the back pocket gives geological, altitudinal and rainfall data.

Mr Ellis is to be congratulated on this meticulously produced volume, with its charming dust-jacket portraying species of especial Welsh connection. Not only British and Irish botanists will be happy to own and use such a splendid production, but surely many further afield will greatly profit by its possession. And regular supplements are promised by **NMW**.

REFERENCES

Hyde, H. A. & Wade, A. E. (1934). *Welsh flowering plants*. Cardiff.
Hyde, H. A. & Wade, A. E. (1957). *Welsh flowering plants*,2nd ed. Cardiff.
Stace, C. A., ed. (1975). *Hybridization and the flora of the British Isles*. London.

A. P. Conolly

Plant variation and evolution. D. Briggs & S. M. Walters. Pp. xvi+412, with numerous text figures. Cambridge University Press, Cambridge. 1984. Price £30.00 (ISBN 0–521–25706–9); paperback £9.95 (ISBN 0–521–27665–9).

It is now just over 15 years since the first edition of *Plant variation and evolution* appeared (reviewed in *Watsonia*, **8**: 179–180, 1970). Deservedly, it became a best-seller in schools, colleges and universities on both sides of the Atlantic, and it has been sorely missed since it went out of print. Both teachers and students, as well as keen amateur botanists, will welcome the appearance of the second edition.

The first half of the book remains much as it was in the first edition, very few alterations of note having been made. In these chapters, the reader is given a historical introduction, beginning from the 17th century, to the work on the patterns of variation found in plants. I like this Baconian approach because in many ways the uninitiated student is in the same position as the early researchers regarding an understanding of the variation we see around us. Enlightenment by means of a historical perspective allows a deeper appreciation of the subject, and I for one certainly find it refreshing to begin the topic with a discussion of oaks and ashes rather than with coils of DNA.

The second half of the book has largely been rewritten but still covers much the same ground as before, viz. breeding systems, speciation, infra-specific variation and its analysis, taxonomy and biosystematics, and some general points on evolution. The subject matter unfolds neatly, and the well-written text leads the reader on from one fascinating topic to another. A further strong point of this book is its detailed, critical discussion of well-chosen examples. The only major criticism I have is that the book fails to deal properly with what has probably been the single most important advance in the study of plant variation since about the time the first edition was published. I refer to the development of enzyme electrophoretic techniques to quantify gene frequencies. Although these techniques are described in the book, their application and the results obtained are virtually ignored. The authors claim (p. 324) that "The study of plant populations by isozyme techniques is in its infancy and perhaps it is too early to make any firm generalizations. . . .". I find this hard to swallow; these studies have been going on for 15 years now and, in this age of rapid scientific advance, a number of critical evolutionary questions have been addressed with a fair measure of success. For example, we can now estimate the heterozygosity and allelic distribution of genes in natural populations, we can get estimates of the genetic distances between populations, we can also get estimates of outcrossing rates, and so on. To omit such information, which is so obviously relevant to the subject matter of this book, was a serious mistake and reflects in part the unease with which the book looks over the fence it shares with population genetics. The authors have chosen to concentrate primarily on an approach based on 1930s-style genecology, and I wonder if they have not overdone the ecology rather, at the expense of the gene.

On the whole however, the book is a good, introductory, student text and deserves to be read widely, not only by students and teachers, but also by keen amateurs (particularly B.S.B.I. members); indeed the final chapter contains hints on how amateur botanists can contribute to the study of plant variation.

In its production, the second edition has a larger format than the first; unhappily, however, it lacks the latter's colour pictures, apparently for reasons of economy. This being the case, I would have thought that Cambridge University Press would have taken more care than they have in the reproduction of the black and white illustrations: many of them are blotchy and/or indistinct in places. I did laugh, though, at Fig. 5.2, which apparently illustrates three *Cineraria* colour variants – all in glorious black and white! (You need the colour picture on the cover to see them properly). There are also two rather enigmatic blank spaces on pages 285 and 287. The paperback is a good buy at £9.95, but the hardback at £30 is overpriced, and a little consumer resistance would not go amiss, in my opinion.

R. J. GORNALL

Ponds and pools – oases in the landscape. K. Kabisch & J. Hemmerling. Translated by Ilse Lindsay, revised by Joan Watson. Pp. 261, with 187 black & white photos and numerous text figures. Croom Helm Ltd, Beckenham, Kent. 1984. Price £8.95 (ISBN 0–7099–1545–4).

This is an unusual and refreshing book describing the life of ponds and pools – those shallow-water habitats that are so often neglected in favour of larger, perhaps more spectacular, rivers or lakes. Despite the admitted transient nature of shallow water, there is a very strong conservation message which is admirably portrayed alongside graphic descriptions of how man continually destroys ponds and pools unnecessarily.

The book is divided into four, rather arbitrary and obscure sections, but all make fascinating reading. There is a clear understanding of what life in ponds and pools is all about, and few books have expressed the intricacies so delightfully. For some tastes the writing may be too poetic, yet within the graphic descriptions are hundreds of throw-away facts and snippets of information. For the keen botanist the book may be disappointing, because plant life is placed in the back seat whilst animal life is placed firmly in the driving seat throughout. Details of plant species are rudimentary, but there are interesting details of seral development by plants that naturally destroys ponds.

Ponds and pools should find its way into most school and university libraries. For 'A' Level and first-year biology students studying aquatic ecology this book should be the most readable of the set of books they 'must' read. It is unfortunate that it is printed only in hardback at a price that is beyond the pocket of all but the most enthusiastic student. As a reference work it is not the most easily used book, since it is not organized or referenced to enable the reader to pick it up and find the desired information tucked away within it.

Few botanists will be seduced into buying it unless they have a great interest in pond wildlife in general. This is due to its zoological bias and the difficulties encountered when trying to use it as a reference work. However it will undoubtedly appeal to a much wider readership due to its flowery literary style and readable presentation of interesting information.

N. Holmes

Plant science & scientists in St Andrews up to the middle of the 20th century. J. A. Macdonald. Pp. 57 with 6 black & white plates. Printed for the author by Quickprint, 14a Argyle Street, St Andrews. 1984. Price £2.50.

This little book brings together a great deal of information on the nature, structure and funding of botanical investigations in St Andrews during the first half of this century. It has obviously been a labour of love, involving much painstaking search through diffused and ephemeral sources such as local newspapers of the time. For those who, like the reviewer, participated at least briefly in the functioning of the Department of Botany during this period, the portraits and brief biographies will bring back vivid memories of the personalities involved.

Inevitably, from the nature of the source material, this account is somewhat disjointed. The end of this period saw the re-opening of the Gatty Marine Laboratory and the beginning of the marine algal research carried out by Dr Helen Blackler (1902–81), which perhaps deserves greater mention.

Professor Macdonald gives us a factual insight into the conditions under which the early plant scientists laboured; this should make us respect their accomplishments the more.

D. E. G. Irvine

Russian-English botanical dictionary. P. Macura. Pp. 678. Slavica Publishers Inc., P.O. Box 14388, Columbus, Ohio 43214, U.S.A. 1982. Price not stated.

Botanists needing to deal with Russian taxonomic literature have been lucky to have at their disposal the *Russian-Latin dictionary for botanists* by Kirpichnikov and Zabinkova (Nauka, Leningrad, 1977), but an equivalent work relating to English has hitherto been lacking. The present work fills the gap. With respect to less specifically botanical words that may be met with, it is deficient in its treatment of adverbs, prepositions and conjunctions; but a particularly useful feature is its coverage of Russian common names, including the Russian 'binomials', often employed in the titles of semi-technical and applied botanical literature. Some of the 'English' equivalents seem strange to the British ear, and may be more meaningful across the Atlantic; but scientific generic and specific equivalents are fortunately also given.

My only criticism is that the title is misleadingly too inclusive; the work covers very well the terminology of morphological botany, but botanists whose interests are mainly anatomical, genetical, ecological, physiological or biochemical will not find their needs met here.

C. Jeffrey

A colour atlas of poisonous plants. D. Frohme & H. J. Pfänder, translated from the German by N. G. Bissett. Pp. 291, with 138 colour and 120 black & white illustrations. Wolfe Publishing Ltd., London. 1984. Price £30 (ISBN 0–7234–08394).

The aim of this book is laudable. It is intended not only to inform the public but also to guide doctors and indeed pharmacists, who in the course of their modern training learn virtually nothing about plants and their effects, be they beneficial or detrimental to man's health. It is a very attractive work, well laid out and beautifully illustrated in both colour and black & white, although, alas, the leafsilhouettes at the back would serve a better purpose as lampshade decoration, since, in the view of some of my colleagues, their instructive value is doubtful.

So far so good. Having paid the extortionate price for one's enlightenment one wonders what harm *Corydalis cava*, a plant virtually absent from these shores, can do. Well, the text makes it clear: "Cases of poisoning by *Corydalis* plant material have not so far been reported and are unlikely". But the height of eccentricity has yet to come. Under the heading *Adonis vernalis*, to which (please note) a whole page is devoted, it is stated "poisoning is hardly likely and is not mentioned in literature", and for the other species of the genus ". . . poisoning is even less likely". For the Baneberry (*Actaea spicata*), one reads, ". . . the toxic principle, does not occur in the plant nor do other highly active constituents, so that poisoning after eating the fruits is unlikely". Having still in mind the title of the work, and most people buy a book for what the title indicates, one wonders whether one should not invoke the Trades Description Act when reading under *Physalis alkekengi* ". . . even now there is no certain information on constituents which might be responsible for possible toxic effects" and, later on, ". . . it is probable (sic!) that the ripe fruits, at least of the Cape-gooseberry can be considered harmless". There are at least five more examples of this kind which could be quoted verbatim, e.g. the Crowberry (regarded by many as a delicacy), the Cornelian Cherry (what a fine fruit for juices and jams!) and the Oregon Grape (pronounced harmless in the book). Admittedly, perhaps with the exception of Sea-Buckthorn (the reviewer eats the fruits by the handful), most of the described plants contain some active ingredients to a varying degree, but should they be classified as poisonous? Moreover, there are other species of a similar nature (e.g. *Oenothera* and *Tanacetum*) which are not included at all. Of course there are the poisonous heavyweights, and they are treated thoroughly in this work. Each species is concisely described, its chemical make-up given and, most important, the symptoms of poisoning indicated as well as treatment. Diagnostic features, both macro- and microscopical, are provided for each species in order to facilitate speedy identification in an emergency. But was it necessary to overload the book, as just indicated, at the buyer's expense? The inclusion of some houseplants, especially the notorious *Dieffenbachia*, is certainly welcome. The list of general literature and an exhaustive bibliography on the subject of poisonous plants and poisoning are, at least to the reviewer, the most valuable aspect of this book. The translator has declared a number of species 'official' by falling into a linguistic trap: the German "officinell' actually means officinal (included in the pharmacopoeia). Despite its short-comings the book can be recommended, but only at a greatly reduced remainder price.

E. LAUNERT

The European garden Flora, volume 2, Monocotyledons (part 2). Edited by S. M. Walters and nine others. Pp. 318, with 25 figures and one map. Cambridge University Press, Cambridge. 1984. Price £30.00 (ISBN 0–521–25864–2).

"The present Flora . . . attempts to provide a scientifically accurate and up-to-date means for the identification of plants cultivated for amenity in Europe", "outside botanic gardens and specialist collections". "The needs of the informed amateur gardener have been borne in mind as well as those of the professional taxonomist". But who cultivates, among many similar examples, *Epipactis phyllanthes* or *Brachypodium sylvaticum*?; and there is even a key to the Lemnaceae ("rarely cultivated" indeed!).

This work might not be expected to be of much assistance to those who work solely on plants wild in Europe. Nor indeed in considerable measure is it. Here I should declare a personal interest, since the idea of this work started with an outline I put to Dr Walters. But subsequently the decision was made to include plants grown under glass, which meant a large expansion in the coverage, and over half this volume is taken up with orchids, nine out of ten genera of which are in no way hardy. Elsewhere too, most of us will find numerous unfamiliar genera, families even.

All the same, there is useful material here for B.S.B.I. members, even if they happen not to own a garden or a greenhouse; for many (even so, too few) look on garden plants with a botanical eye. For one thing, there should be help with some of the escaped plants – I noted that *Arum orientale* is said to naturalize readily. Another advantage is in the characters and keys used when they differ from

Flora Europaea, for example in the (much simplified) orchid genera, wherein may lie just the clue needed.

The work is conceived in much the same way as *Flora Europaea* – this is the first volume to appear. Although handicapped by much less funding, production is of a similar high standard; but the text is now triple column, in a slightly larger type size. All but one of the contributors are professionals. This Flora has the immense advantage over every comparable publication for many a long year of being in taxonomic, and not alphabetical, sequence, keyed throughout. Names are all in Latin, inevitably in view of the various vernacular ones used all over the Continent. But a few common names creep in. 'Bowles Yellow' is added to 'Aurea' under *Carex riparia* for the glorious variant that E. A. Bowles is said to have found in Wicken Fen, but 'Aurea' only is given under *C. elata* – where Bowles's plant belongs. And were these cultivar names in Latin form published before 1959, to make them valid?

Authors of Latin names are set out in full, which will de-mystify many a gardener, but only one citation is given when there is an 'ex'. This may be permissible under our Code of Nomenclature, and look less daunting to gardeners, but it verges on the abstruseness of the zoological one. There is an improvement on *Flora Europaea* in that there are 25 whole pages of line drawings to show certain main characters and technical terms, but there are none of individual plants.

A difficulty found by most if not all contributors was the extreme scarcity of herbarium specimens of garden plants; no gardener can contemplate pressing, drying, killing, what he cherishes alive. But how many botanists ever press garden flowers, even common ones? Enough said?

Last but not least, such was the eventual time-table, that no author was sent a proof of his contribution. In the account of the bamboos (at least), drastic editing has resulted in the introduction of error and misrepresentation of the author's views.

All the same I greet this great work warmly, and strongly recommend that each volume be acquired as it appears, so as to spread the not unreasonable cost.

D. McClintock

An Irish flower garden. E. C. Nelson, illustrated by W. Walsh. Pp. 218 with 4 colour and 23 black & white plates. Boethius Press, Kilkenny. 1984. Prices: soft covers £8.85 (ISBN 0–86314–095–5); hard covers £15.20 (ISBN 0–86314–094–7); limited edition, half leather £62.00 (ISBN 0–86314–096–3).

This is an agreeable discourse on the history and background of some of the numerous plants with specially Irish connections. Even so, 'some' amounts to about 120, and Dr Nelson's researches have revealed many fascinating facts and sidelights. Admittedly the theme is garden plants, but many of these are good Irish natives, e.g. *Arbutus unedo*, *Allium babingtonii*, *Daboecia cantabrica*, *Rosa* × *hibernica*, *Saxifraga hartii* and *Salix hibernica* (duly, critically assessed), or are variants from the wild preserved in gardens, such as nearly all the heathers or f. *spiralis* of *Juncus effusus* (which, coming 'true from seed' and also growing in Orkney and Shetland, should not be termed 'Spiralis').

But any plantsman worth his salt will not restrict his reading to plants emanating from our islands, for there is much to enjoy about the others, many familiar. There are four full-page plates, in one of which the colour does not well match the original, and 23 black & whites. In all these Mrs Walsh has depicted the plant with her typical elegance, but the lack of colour prevents some of them from being fully distinctive. Oddly, their captions are not on the same page, but at the bottom of the subsequent one, which is otherwise completely blank.

This is an excellent source book and, happily, fully indexed.

D. McClintock

The wild flowers of the British Isles. I. Garrard & D. Streeter. Pp. xi+295, with 102 colour plates. Macmillan (London) Ltd., London & Basingstoke. 1983. Price £14.95 (ISBN 0–333–32679–2).

In the increasing market for books that fill the gap between coffee-table books and working textbooks, there is probably space for more good illustrated Floras; and we now have this book published at the same time as *The new concise British Flora* by W. Keble Martin, with text revised by D. H. Kent. Any review must, I feel, compare these two volumes, which have different strengths and weaknesses.

Why are trees, grasses and sedges supposed to have no flowers? This is particularly sad as Ian Garrard, the artist, is a superb illustrator of trees; if there were technical reasons or, dare I breathe the heresy, financial reasons, could we not have been told? In Keble Martin the sedge plates are definitely among the best in the book, even if the text in the revised edition does contain one of its few errors (*Carex cuprina* being unnecessarily substituted for *Carex otrubae*).

Another general quibble in Garrard & Streeter concerns the colour reproduction of the plates. I was lucky enough to see some of the plates at a B.S.B.I. Exhibition Meeting, and all who saw them will agree that they were magnificent, being especially good in the area of small inconspicuous plants (Caryophyllaceae, Cruciferae and Euphrasias). However, in the published book some of the pinks, purples and blues are simply bad. If I could reproduce horticulturally the colour of the Fritillary flower shown on Plate 94, then I am sure I could make a fortune. Nevertheless, and very importantly, the shades, textures and various hues of green of the leaves are among the best I've ever seen. This, taken with the technique used to illustrate water plants (a little strange at first sight but it grew on me at least), does much to counteract some of the other faults.

The book's real strength lies in the detailed and very accurate plates of some of the most critical genera in the British flora, where the artist has been helped by many experts and referees in critical groups such as *Alchemilla* (Dr Max Walters, not Max Miller as reported in one review), *Euphrasia* (Dr P. Yeo) and the Orchids (overseen by D. Lang).

Artistically and for use, the plates are much better laid out than those in Keble Martin, much less crowded and with each plant shown separately; but of course gremlins do creep into the labelling. On Plate 70, *Pinguicula vulgaris* was labelled *Pinguicula alpina*, and in the splendid orchid plates the Early Purple Orchid has been named in English and Latin as the Early Spider Orchid, presumably a *lapsus calami*.

A very few of the illustrations simply don't work and don't resemble the plants. The two worst ones, in my opinion, are *Centranthus ruber* on Plate 79, which is much too fleshy and thick-looking, and the picture of *Viola cornuta* on Plate 15, which is shown with a virtually rotate corolla and heavily veined petals. The drawing in no way resembles the plant in life. Colour can be a great aid to plant identification, and a great opportunity has been lost by the use of virtually identical reds for the poppy plates and identical yellows for the gorse species.

The selection of some of the plants illustrated leaves something to be desired. It is almost as if, having decided to omit the grasses, sedges, trees and shrubs, the barrel had been scraped to make up the numbers with many rare or suspect introductions such as *Cistus incanus*, Pl. 7 (see A. L. Grenfell in *B.S.B.I. News* **34**: 22 (1983)), and *Papaver lateriticum*, which Eric Clement maintains as being recorded in error for *P. atlanticum*.

David Streeter's text is a model of brevity, with useful little snippets added in brackets to aid separation of closely related species, and is adequate within its obviously very tight remit. The emphasis is ecological rather than morphological, unlike Keble Martin (all editions), in which more details of morphology are included.

Now, despite all these apparent carping criticisms, this is a very important book and is well worth having. It is not a book for the field but perhaps for the car, and certainly one that is worth a place on your bookshelf next to Keble Martin. As to personal choice, mine goes to Keble Martin, for its text especially; but I'm sure that the more artistic will undoubtedly prefer this book.

J. M. Mullin

Atlas der Brombeeren von Dänemark, Schleswig – Holstein und dem benachbarten Niedersachsen. H. A. Martensen, A. Pedersen and H. E. Weber. Pp. 150, with 122 maps. Forschungen und Berichte zu Naturschutz und Landschaftspflege, Beiheft **5**. Hanover. 1983. Price DM 15.00 (ISBN 3–922321–19–4).

This atlas contains maps of the distribution of *Rubus* microspecies in Denmark and neighbouring parts of Germany. Over 50 of the species also occur in Britain, and distinct ecological preferences are visible in the maps. The mapping unit is curious, since it is rectangular and does not correspond to other British or European mapping schemes, but to German national maps. The quality of reproduction of maps and text is excellent.

R. J. Pankhurst

The diversity of crop plants. J. G. Hawkes. Pp. vi+184, with 37 text figures. Harvard University Press, Cambridge, Massachusetts, etc. 1983. Price £17.00 (ISBN 0–674–21286–X).

This book developed from a series of lectures given at Harvard University in 1977, but the references have been updated to 1982. The seven chapters cover: characters which distinguish domesticated plants from their wild progenitors; origins of agriculture; the work of de Candolle and Vavilov; the study of diversity within crops; the plant breeder's need for and use of diversity; techniques for collecting and storing this diversity; and the international co-operation which has resulted in establishment of gene banks for the world's major crops.

This story has been told before, though in journal articles rather than book form. Nevertheless, I was left wondering at whom this book is aimed. Research workers in this field will already be familiar with most of the concepts discussed, though Professor Hawkes' final chapters are a useful review of some not universally accessible IBPGR publications (acronyms are impossible to avoid in this area, but Professor Hawkes provides a useful list of them). As an undergraduate text, this book is too circumscribed to constitute much more than supplementary reading. It also has to compete with Harlan's earlier but more extensive *Crops and man* (1975), and with Frankel & Soulé's recent *Conservation and evolution* (1981), which provides a fuller genetical background to the understanding of diversity. However, unlike the latter authors, Professor Hawkes demands no great *a priori* knowledge of his readers. He writes clearly and concisely and should carry readers at any level effortlessly with him.

Much of the previous literature on crop diversity has been written by those who work with annual seed crops. Professor Hawkes adds the perspective of one who has worked mainly with a vegetatively propagated crop and also has supervised research work of students from many different countries on a multitude of different crops. He makes occasional errors concerning crops with which he is less familiar. The sweet potato is hexaploid, not tetraploid. The student who wrote in my exam that the main types of dry fruit are a locule, a lomentum and a rachis, will be encouraged that Professor Hawkes also has trouble with *Arachis* fruits, describing peanut pods as capsules when they are in fact indehiscent legumes or lomenta.

A price of £17.00 for a slim book suggests a self-fulfilling prophesy of limited sales. It is a book which many people, both professional botanists and those simply interested in plants, may read for information and enjoyment, but are likely to think twice about purchasing at the hard-cover price.

REFERENCES

Frankel, O. H. & Soulé, M.E. (1981). *Conservation and evolution*. Cambridge.
Harlan, J. R. (1975). *Crops and man*. Madison.

B. Pickersgill

Dispersal and distribution. An international symposium. Edited by K. Kubitzki. Pp. 406, with 100 text figures. Sonderbände der Naturwissenschaftlichen Vereins in Hamburg, 7. Verlag Paul Parey, Hamburg and Berlin. 1983. Price DM 108 (ISBN 3–490–13996–8).

Although much ink has been spilt over the topics of dispersal and distribution individually, there have been very few (if any) comprehensive attempts to consider them together. The symposium held under the above title in the University of Hamburg in June 1982 included papers on a wide range of cognate subjects, most of which are reproduced in the volume under review.

An introductory contribution by R. Y. Berg, discussing general principles and basic models of dispersal, raises the question of how important long-distance dispersal is in the origin of disjunct areas of distribution. Berg points out that those in favour cite the theoretical importance of the one-in-a-million chance (given sufficient time) and the large amount of indirect evidence of its occurrence; whereas those against emphasize distribution patterns and dispersal restrictions that it cannot explain, and deprecate the use of chance as the basis of a scientific theory. Carlquist, having provided strong evidence in favour of long-distance dispersal from California to Chile by means of birds, then draws the (to me) unwarranted conclusion that "such dispersal may have had a preponderant influence on current angiosperm distribution patterns". Van Zanten, more reasonably, concludes that long-distance dispersal in Bryophytes is more important at the species level than for genera, where plate tectonics are more likely to account satisfactorily for the disjunctions.

Long-distance dispersal is also favoured by White as an explanation of distributional patterns in the Afromontane flora, the various mountain groups being likened to continental islands. Subsequent contributions are mostly concerned with the effect of dispersal mechanisms on distribution in systematic groups (e.g. Urticales, Lecythidaceae, Chrysobalanaceae, Mesembryanthemaceae, Bignoniaceae) or plant communities (e.g. neotropical forests, dry Brazilian scrub, Amazonian savannah, arid habitats); but there is a fascinating section on special vectors of diaspores, such as ants, bats and Amazonian fishes. The seeds of some species require a series of vectors, e.g. parrots (on the tree), agoutis (on the ground) and beetles (which bury them).

This is a solid book – solidly packed with data and ideas, not at all dull – that makes fascinating reading. It will provide data to support many pet distributional theories (or otherwise), and it will almost certainly stimulate new ones. Some of the views expressed may seem exaggerated or even outrageous, such as Carlquist's claims for long-distance dispersal or White's implied assertion that the whole flora of Réunion arrived relatively recently across the sea; but it is a most important contribution to an important aspect of both phytogeography and ecology.

N. K. B. ROBSON

Plant Portraits from the Flora Danica 1761 – 1769. Twelve reproductions of plates by Martin & Michael Rossler. Historical and botanical text by William T. Stearn. Pp. 12 with 12 colour plates. The Mendip Press, Bath. 1983. Price £9.95 (ISBN 0–900751–20–7).

Flora Danica was originally published in 17 folio volumes, spanning the period 1762–1883 and containing some 3200 hand-coloured plates. Copies are now rarely seen outside the larger national libraries, and the splendid plates (particularly those of the first 10 volumes) are largely unknown to many present-day botanists. The slim folio volume now to hand reproduces 12 plates from early fascicles of the original flora together with an introduction to the background and history of the work. The plates, which feature in the main common British species, are excellent reproductions and faithfully represent the style and character of the original hand-coloured engravings. As is to be expected from the pen of Dr Stearn, the historical introduction and extended botanical notes to each plate are lucid and scholarly. The bibliographical background of *Flora Danica* has long been somewhat confused, and Dr Stearn has collected together a good deal of fragmented knowledge which will be of interest to the student of European Floras and lovers of fine botanical illustration.

The rather meagre offering of only 12 reproduced plates in the present volume is no doubt due to the high cost of colour printing, but the book should serve as a reminder of the vast storehouse of botanical artistry contained in the finely illustrated European Floras produced in the late 18th and early 19th century.

M. WALPOLE

The natural history prose writings of John Clare. Edited by M. Grainger. Pp. lxii+397 with 7 black & white plates and 5 maps. Clarendon Press, Oxford. 1984. Price £35.00 (ISBN 0–19–818517–0).

John Clare, who has been described as a peasant poet, was born in 1793, the year Gilbert White died. If Clare's *Natural History of Helpston* (Northamptonshire) had been completed, we are told, the village might have been as famous as White's Selborne. Clare is depicted as a poor man, initially struggling, with the aid of various patrons, to get his verses published. His first poems were descriptive of rural life and were published when he was 27. He exchanged letters, notes and verses on natural history with many correspondents of a wider social range than his status in life might suggest possible. He was virtually self-taught in all aspects and, judging from the books he owned or borrowed, was widely read. His poems have been republished several times but his natural history prose is less well known.

Margaret Grainger's book successfully alters this. It is a very full compilation with some of the most detailed footnotes I have ever seen. She indicates that she thinks it would be perverse to omit some of the literary prose, although not connected with natural history, since the two topics are so interwoven. Even so, some of the entries make me wonder why they were chosen, other than for completeness – "Monday 10 August 1828. A Favourite Tabby Cat Got killed to day either purposely [sic] or by accident I cannot make out which" is the only entry from Northampton manuscript 17 and this, together with some notes on it, occupies one page, leaving two-thirds blank.

Reading the entries in his journals or letters, one realizes the attention he paid to detailed observation of nature; in fact he eschews the "closet naturalist". He also noticed the damage caused to the countryside by the newer developments like the proposed "iron rail way" which he felt sure would destroy a favourite patch of orchids. Virtually his whole life was spent in Northamptonshire, and he rarely went beyond the limits of his own village of Helpston.

Broadly speaking, the book consists of a chronological account of the birds and plants around Helpston but it is also very revealing on horticulture and has entries of considerable value. His observations on plants were used by Druce (1930) and Perring (1955) as a source of information on the local flora, although some of the earliest records of a number of plants (*Silene alba*, *Linaria vulgaris* and others) are from manuscripts which were not available to these authors. A long section is devoted to Clare's bird-list with his observations on their status.

Throughout the whole work the editor's detailed footnotes appear; and these, together with the glossary, appendices (18 pages), maps and a very detailed and accurate index, make this a monumental work of reference. There are over 150 footnotes in a random selection of 20 pages; but I found their numbering unnecessarily complicated, with two sets of identically numbered footnotes on the same page.

There are only seven plates and five maps in this very expensive book. It lists some drawings by Clare but only one of these is used; the rest of the illustrations are pages from his notes. Possibly his drawings were not suitable for use, but this is not indicated.

Although not an easy book to read, the thoroughness of the work and the careful editing make this a comprehensive reference work which will not be surpassed.

REFERENCES

Druce, G. C. (1930). *Flora of Northamptonshire.* Arbroath.
Perring, F. (1955). John Clare and Northampton plant records. *Proc. bot. Soc. Br. Isl.*, **1**: 482–489.

P. H. Whalley

A camera in the garden. H. Angel. Pp. 160, with 81 colour plates and 1 text figure. Quiller Press, London. 1984. Price £9.95 (ISBN 0–907621–34–1).

A camera in the garden covers just about every imaginable aspect of garden photography in colour, from the obvious garden and greenhouse scenes, through plant portraiture and 'design-in-nature' to water and garden architecture and monuments.

The general approach is to catalogue the things that may be done with the camera in the garden and then to show how to do them. Many of the ideas are exemplified by the numerous lovely colour photographs, but others are left to the imagination. The pictures, many of them quite superb, are both a feast and a challenge.

A great deal in this book is relevant to the interests of the field botanist with a camera, who will probably find in it ideas for extending his scope (the plant portraiture sections range from alpines to trees). The 'how to do it' side seems comprehensive; the author allows the possibility that the reader may be using very simple equipment, while making innumerable points about taking pictures, amongst which the more experienced photographer is sure to find something helpful.

Readers of *Watsonia* interested in photography who feel it is time they got some help will, I think, find this book, which is excellently produced, a good buy at £9.95. If they are interested in gardens too, they *ought* to get it. Those that do will appreciate the care that Heather Angel has taken with plant names and will be grateful for her wide knowledge of natural history.

The book includes a glossary, notes on equipment and on monochrome photography, a fault-diagnosis table, a list of societies, a bibliography, a table of gardens to visit in Great Britain with indications of their special features, a list of books and addresses for readers wanting to photograph gardens abroad and an index.

P. F. YEO

Obituaries

JEREMY NICHOLAS BARTON MILTON
(1959–1984)

Writing a short note for *Watsonia* should normally be a fairly straightforward matter of expressing a discovery or observation in clear orderly terms. The initial work may have raised all kinds of excited feelings, but its successful communication in a scientific journal needs more calm reason than emotion. This is obvious, but after many trials we found ourselves unable to write this short memorial to Jeremy Milton without using a more informal, feeling tone. We trust that the exceptional quality of his life will excuse this exception to the usual *Watsonia* style.

Many B.S.B.I. members may never have met Jeremy. One of the youngest ever officers of the Society, he held the position of Field Meetings Secretary for barely a year before his shocking death in a road accident on 15th May 1984, aged 24. These people will at least be able to read notes by him in forthcoming issues of *Watsonia* and *BSBI News*, and may have the benefit of meetings arranged by him; but those who were lucky enough to have known him will, like us, miss for ever his extraordinary good nature and unstinting energy, his talent for seeing what was significant in even the most ordinary habitats, his ability to make field work, however routine, full of thrills and amusement, and his wonderful quickness with ideas.

He was undoubtedly a dedicated botanist from an early age, when he began botanizing round his home and school in Oxfordshire. He read Botany at Oxford, and for the past 1½ years had been working for his Ph.D. at Queen Mary College, London, under Professor Jeffrey Duckett, who speaks highly of Jeremy's research. The subject was the possible allelopathy of some pteridophytes (in particular *Equisetum* species), that is, their ability to produce substances that depress the vitality of plants in close competition with them. An abstract summarizing this work will appear later this year in *Phil. Trans. Roy. Soc. Edin.* (J. N. B. Milton & J. G. Duckett, 'Potential allelopathy in *Equisetum*'); and recently Jeremy had made a fascinating discovery suggesting that spores (of ferns, *Equisetum* and Bryophytes) contain a comparable substance or substances that may stimulate their germination in crowded conditions. Such productive research had put him well on the way to being a plant scientist of high calibre. We can only take some comfort from the fact that his work stands and can be communicated, and will be continued.

We were more familiar with him as a field botanist than as a laboratory worker, remembering him scaling the Portland cliffs for inaccessible *Adiantum*, or sodden with black mud after mucking out a Buckinghamshire pond, wearing a badge saying 'Save Our Starfruit'. Expeditions with him were always a joy: there were perennial silly jokes: "Oh look, Jerry, *Equisetum arvense*!" to greet the first horsetail of the day; the unforgettable sight of him leaping in the air, arms and legs flying, when something nice turned up; the 'shriek index', which measured how special a plant was; the daring climbs and crazy endeavours; and of course, through all the fun, there were good discoveries – *Trifolium occidentale* in North Devon, *Eryngium campestre* in South Hants, *Cyperus fuscus* in the New Forest. His energy was phenomenal. A 'night bird' with a great fondness for good tea, he was able to make great progress with personal projects as well as his formal research, in particular in the no-man's-land of *Hieracium*. His contributions, when published, will be of lasting value. Midnight phone calls about hawkweeds might seem something life could well do without, but being from Jerry they actually left one inspired rather than yawning and grumpy! Bryophytes also gave him great pleasure (he was more than competent in this other difficult field), and a number of good records from the East End of London testify to his enthusiasm for aliens.

Memories, affection, gratitude for his companionship and his example, all these could fill books, as could an enumeration of the ways in which his death has caused a loss to botany. In his few years he actually achieved a great deal; but it was obvious that even more wonderful things were going to come next, both in academic research, and in the ways he was both a conscientious and able officer, and an excellent public relations agent. He had the eye for detail and appreciation of shades of meaning, both taxonomically and ecologically, which make a really good botanical observer. Though on occasional 'twitching' expeditions the shriek index might almost reach the top, he never came back without meticulous notes that acknowledged the rarity in question only as part of the appropriate community and habitat. Studies in the British flora were already gaining from his contributions, and he had shown great interest in more distant fields, having taken part in two expeditions to East Africa.

The B.S.B.I. have shown their respect by asking us to write these notes in his memory for their most formal journal. His family, together with friends and colleagues at Queen Mary College, have subscribed to a fund that will establish a prize in his name in the field of plant biology/ecology. As his friends, we can only say how glad we are to have known and adventured with Jeremy, how grateful we are for the work that he has left to use or continue, and how we trust that his example will make us better botanists too.

A. J. Byfield & R. Fitzgerald

MARK CHRISTOPHER CAIGER SMITH
(1933–1984)

The many members who heard Dr Smith speak on the work of the Bristol University Botanic Garden on the occasion of the 1983 Annual General Meeting will have been shocked at the news of his sudden death only ten months later, at the early age of 50.

Mark Smith's dedication as a plantsman was so whole-hearted and complete that few can have suspected that he came to professional botany only comparatively late in life. Although he had specialized in natural sciences during his schooldays at Stowe, it was economics that he chose to read when he went up to King's College, Cambridge, after National Service. That led into an initial career as an investment analyst, first with the Prudential Assurance Company and then with a leading firm of London stockbrokers, in which he quickly rose to become head of the research department and had the prospect of an early partnership. City life, however, repelled him. Always a hankerer after physical adventure, preferably under arduous conditions in far-off places, he had seized the opportunity already of the break between these jobs to journey round Africa by motor-bike. Immersion in the Africa flora, and particularly in that of the Cape, served to intensify his lifelong passion for the plant world; and it was only after a good deal of heart-searching that he decided to return to England. Exiled among bricks and mortar once again, he made up for the aching lack of garden by filling his bleak bachelor bedsitter with antique Victorian bell-glasses, each of them housing some lovingly chosen exotic. It was in these years that he first came into touch with the B.S.B.I., attending one or two field meetings in the London area as a guest.

In 1962, having finally found London more stifling than he could bear, he moved to Bristol to work as Group Economist to E. S. & A. Robinson, the leading manufacturers of packaging materials. But while he revelled in having escaped to the West Country, life as a businessman continued to pall. A subscriber to the idealist view that no one should work away at an occupation unless totally committed to it, he accordingly resolved to return to university with a view to equipping himself for a botanical career. A courageous decision for anyone in their mid-thirties on intellectual grounds alone, this was the more courageous for the fact that he was by then a husband and a father. The three years needed to acquire his first degree, which he took with First Class Honours, were to be followed, moreover, by a further lengthy period of doctoral research. His work for that, a computer study of the variation and taxonomic relationships of *Sempervivum* species of Spain and the Pyrenees – a very characteristic choice – led to an exhibit at the joint B.S.B.I./Linnean Society conference in 1971. The year before that he had eventually become a B.S.B.I. member; but British field botany was never to be more than a very secondary interest, and his involvement in the Society's activities remained disappointingly marginal.

After gaining his doctorate he applied for two University posts, but with little real enthusiasm. In 1972, however, the perfect career opening occurred for someone of his particular bent and abilities: the revitalizing of the Bristol University Botanic Garden. His appointment to the Garden staff was soon followed by the retirement of the Head Gardener, whereupon Mark assumed control. His immense resources of energy and innovation transformed the Garden to the extent that he became synonymous with it; and his success was not just narrowly horticultural, for the thriving League of Friends, formed in 1976, also remains as a monument to his dynamism. Perhaps his keenest interest was in alpines (he was a founder member of the Bristol Branch of the Alpine Garden Society), which he had the eagerly-seized opportunity to collect on a visit to New Zealand, on a grant awarded by the Stanley Smith Horticultural Trust; but a visit to Bracken Hill would also betray more than a passing involvement with *Paeonia*, *Cistus* and *Impatiens*.

Charming and courteous, unquenchably enthusiastic, Mark was not only respected by all who were fortunate enough to know him, but someone to whom they invariably became devoted. We offer our deepest sympathy to his wife Bridget and to their three children.

D. E. ALLEN & A. L. GRENFELL

Reports

ANNUAL GENERAL MEETING, 19TH MAY 1984

The Annual General Meeting of the Society was held in the Meeting Room, The Linnean Society of London, Burlington House, Piccadilly, London at 12 noon, with 77 members present. Mr J. F. M. Cannon, President, taking the chair, opened the meeting with the very sad report of the death of Jeremy Milton (Honorary Field Secretary) in a tragic road accident the previous week. A letter of condolence had been sent to his parents, and the Society would be represented at the funeral.

The adoption of the Minutes of the last Annual General Meeting, as published in *Watsonia*, **15**: 59–60 (1984), was proposed by Professor J. P. M. Brenan and unanimously approved by the meeting. Apologies for absence were read.

REPORT OF COUNCIL

Presenting the Report of Council for the calendar year 1983, the Honorary General Secretary offered a sincere apology to Miss G. M. Haines who, although reported as having died, was in fact alive and well. The Secretary had been in contact with Miss Haines, who had assured us of her unruffled acceptance of our apology.

The President drew attention to the deaths during 1983 of two eminent foreign members, Professors T. W. Bocher and J. L. van Soest, as well as to the deaths of seven members of more than 20 years' standing. The adoption of the Report, which had been circulated to members, with the reinstatement of Miss G. M. Haines, and three spelling corrections, was proposed by Dr C. P. Petch, seconded by Mr A. O. Chater and carried unanimously.

TREASURER'S REPORT AND ACCOUNTS

The Treasurer, presenting his Report, commented on the current very high costs of postage, and noted that the use of first class mail for the recent distribution had been an unauthorized action by the printer.

In reply to a question by Mr D. E. Allen, the Treasurer defined Administration Expenses as those of membership records and subscription collection, and General Expenses as miscellaneous secretarial items. The *Flora of Breckland* continued to be a drain on our assets.

The adoption of the Report was proposed by Mr R. W. David, seconded by Mr D. H. Kent and carried unanimously.

ELECTION OF VICE-PRESIDENT

The President welcomed the nomination of Mr E. C. Wallace, who had acted for the Society in many capacities since he had joined as a member in 1932.

ELECTION OF OFFICERS

The following officers had been nominated for re-election: Mrs M. Briggs M.B.E., F.P.S., F.L.S., Honorary General Secretary; Mr M. Walpole F.C.A., F.L.S., Honorary Treasurer and Miss J. Martin (now Mrs J. Robertson), Honorary Meetings Secretary; these officers were re-elected and thanked with applause. The following Honorary Editors were also re-elected and warmly thanked for their considerable voluntary work for the Society: Drs J. R. Akeroyd F.L.S., S. M. Eden, R. J. Gornall and N. K. B. Robson F.L.S.; Dr B. S. Rushton was elected (*Watsonia*); Mr D. H. Kent (*B.S.B.I. Abstracts*) and Mr E. D. Wiggins (*B.S.B.I. News*) were also elected, with a proposed amendment to Rule 6.

ELECTION OF COUNCIL MEMBERS

Dr C. J. Cadbury, Dr T. A. Cope, Mr E. F. Greenwood MSc. and Dr N. T. H. Holmes had been nominated and were unanimously elected.

ELECTION OF HONORARY AUDITORS

The Honorary Treasurer again expressed our gratitude to Messrs. Thornton Baker for auditing the Society's accounts and proposed their re-election. This was carried unanimously with applause.

ANY OTHER BUSINESS

There being no other business, the meeting closed at 12.45.

M. BRIGGS

VISIT TO DEPARTMENT OF BOTANY, BRITISH MUSEUM (NATURAL HISTORY) FOLLOWING THE ANNUAL GENERAL MEETING

54 members, who had accepted the invitation to see something of the work of the Department behind the scenes during the afternoon following the Annual General Meeting, assembled on the landing outside the General Herbarium. After an introductory welcome by the Keeper of Botany, Mr J. F. M. Cannon (B.S.B.I. President), the members divided into five groups and were guided to five 20-minute demonstrations in different areas of the Department:

Mr A. C. Jermy – work on the groups in the Cryptogamic Herbarium;
Mr A. O. Chater – the Sloane Herbarium, with special reference to old British collections;
Dr N. K. B. Robson – floristic and monographic work on flowering plants in the Department;
Mr R. J. Pankhurst – the British Herbarium, departmental Flora projects and other activities;
Ms A. Pope – historic material in the Library, with special reference to the British flora.

The programme concluded with an illustrated lecture in the Main Lecture Theatre on *Insects and Plants*, given by Mrs J. Pope.

Great interest was shown by the members present, and all expressed their gratitude to the museum's staff who had prepared and presented the various demonstrations and the lecture.

M. BRIGGS

EXCURSION TO WEST THAMESMEAD AND LESNES ABBEY WOOD, LONDON, HELD IN CONNECTION WITH THE ANNUAL GENERAL MEETING, 20TH MAY 1984

Due to an earlier breakdown in communication, it had been quite wrongly supposed that a visit to the closed parts of West Thamesmead by a party of B.S.B.I. members would be able to help with a habitat survey recently commissioned by the Greater London Council. (In fact the area had been separately surveyed the year before). Nevertheless the GLC was very willing to welcome us, and Mr David Hope of their Ecology Section met us at Abbey Wood Station and took us by land-rover to the site. The rains, which continued all day, had deterred many from coming and the complete journey was done in two trips. However an hour had passed before David Hope had mustered his complete party of 23, by which time *Azolla filiculoides* had already been found in a ditch, new to the metropolitan part of v.c. 16.

Much of Thamesmead is built on ground previously occupied by the greater part of Woolwich Arsenal, though in places there are still relics of an earlier system of marsh ditches. Information about the way the Arsenal used its ground is still covered by the Official Secrets Act but presumably the mounds surrounded by moats, now called 'tumps', which are a conspicuous feature of the area, covered explosives stores. Some of the 'tumps' have been worked into the design of the developed parts of Thamesmead. The visit started at a pair which, for a brief period in the 1970s, were accessible to classes as the 'Twin Tumps Nature Trail'. It was too early in the year for a thorough examination of the slightly brackish water here to be profitable, but the bright green of a small patch of *Juncus compressus* was pointed out at its edge.

From here David led us through dense birchwood and then, crossing a desert of clinker, where the birches are all much younger, a pretty patch of *Erodium cicutarium* was admired, and rosettes of mostly biennial, summer-flowering species were noted for the first time: *Oenothera* spp., *Verbascum* *thapsus* (but not *V. lychnitis* which was present in the 70s), *Inula conyza*, *Erigeron acer* and *Echium vulgare*.

This clinkery ground may eventually be built over but the area to the west, euphemistically called Tripcock Park on the G.L.C.'s plans, will not be. It is extremely polluted with heavy metal residues. David led us up on to a steep-sided plateau from which we could look across an astonishing landscape of broken roofs to the tall sluice-gate of Barking Creek, across a bend in the Thames. The huts were built in separate pits connected by walled passages. On the less dissected part of this plateau were quantities of *Anthriscus caucalis* and *Myosotis ramosissima*, and on the 'scarp' slope *Montia perfoliata* and a *Hieracium* with boldly marked leaves, perhaps *H. liljeholmii* Dahlst., discovered in 1983 on old railway ballast a few miles to the north in Essex by Jeremy Milton, who had been looking forward to this excursion, as to so much else.

For over an hour the party had been within 400 m of the Thames and seen no sign of its presence: now we were led down the bank and out on to the Thames-side above Tripcock Ness to look at a saltmarsh. It is only a narrow fringe below the river-wall but it is now the western limit in London for *Glaux maritima*, *Juncus gerardii*, *Plantago maritima* and *Cochlearia anglica*. Also present in the marsh are *Oenanthe crocata* and *Angelica archangelica*, the fruits of which drift downstream from long-established populations west of London.

This was the end of David's planned itinerary and from here we had to walk back to the security gate by which we had come in. Near the gate there was an opportunity to compare flowering material of *Sisymbrium altissimum*, *S. orientale* and *Erysimum cheiranthoides*.

Somehow everybody who wanted to was able to return to Abbey Wood Station, and there was enough room in cars for us all to have lunch sitting in a car park under the viaduct, from where after lunch, a much depleted party ventured back into the rain. Three habitats were then sampled: closely mown grassland (which at this date offered only abundant *Medicago arabica* and *Stellaria pallida*), Abbey Wood itself, and the low flint walls which are all that remains of Lesnes Abbey. In the wood *Galeobdolon luteum*, *Milium effusum* and the one population of *Allium ursinum* were admired but the one tuft of *Carex strigosa* known since 1967 was not refound. In other woods on the Blackheath Beds farther out of London *Convallaria majalis* is a characteristic (and usually sterile) native; the clump that we found in Abbey Wood was very obviously a recent planting. We almost went out of the wood not noticing abundant *Luzula forsteri* on a bank in one of the enclosures, fenced off to protect the splendid colonies of apparently truly wild *Narcissus pseudonarcissus* which are at their best here in late March. On the Abbey walls there are a few plants of *Saxifraga tridactylites* and three small fern species, but at this time the nearby tea-room had greater attraction. It was generally agreed that the assemblage of plants seen during the day, though perhaps ordinary in some parts of the country, was quite remarkable eight miles from Charing Cross.

R. M. BURTON

FIELD MEETINGS, 1983

ENGLAND

BIRKDALE, MERSEYSIDE. 25TH JUNE

Only nine people attended this meeting to examine the distribution of *Juncus balticus* and hybrids on the Birkdale sand-dunes. However, those attending were grateful to Dr P. H. Smith of the Liverpool Polytechnic who kindly guided the party on the day and was able to demonstrate how *Juncus balticus* had spread on the dunes since its first discovery in 1913. The meeting was therefore a field demonstration of his recent paper (*Watsonia*, **14**: 15 (1984)).

E. F. GREENWOOD

NEW FOREST, HAMPSHIRE. 3RD SEPTEMBER

The unexpected loss of nine accepted participants reduced the numbers to 14, which was the more regrettable as the party had an excellent day. The New Forest is well known for having many plants chiefly found only in northern and western parts of the British Isles; but the surprising interest of this excursion arises from the fact that in the Hatchet Pond area, the Forest contains four quite different habitats within a stretch only two miles long.

The pond itself, together with adjacent small ponds, contained such rarities as *Pilularia globulifera*, *Sparganium angustifolium*, *Elodea nuttallii*, *Littorella uniflora*, *Elatine hexandra* and *Ludwigia palustris*. One of the ponds has been invaded by *Crassula helmsii*. The damp acid heaths and bogs surrounding the pond had such typical species as *Rhynchospora alba*, *Baldellia ranunculoides*, *Scirpus fluitans*, *Cirsium dissectum*, *Genista anglica*, *Chamaemelum nobile* and two *Drosera* species, but also included rarities such as *Lycopodiella inundata*, *Utricularia minor* (in fine flower), *Centunculus minimus*, *Cicendia filiformis*, *Pinguicula lusitanica*, *Hammarbya paludosa*, *Deschampsia setacea*, *Galium debile* and *Juncus foliosus*.

Nearby is an abandoned, wartime airfield on a slightly raised gravel plateau. Was its flora accidentally brought with imported 'fill' or did it come spontaneously to an attractive area of crumbling concrete, or both? Here within feet of acid heath plants were species perhaps more characteristic of the Downs. We saw *Viola lactea*, *Verbena officinalis*, *Erigeron acer*, *Desmazeria rigida*, *Lotus corniculatus*, *Spiranthes spiralis*, *Cirsium acaulon*, *Linum catharticum*, *L. bienne*, *Centaurium erythraea* and *C. pulchellum*. *Sedum album* was abundantly naturalized.

The fourth site, a mile further south, consists of some abandoned marl pits. These exemplify the surprising calcareous patches scattered about The New Forest, and suggest that not all the airfield plants need have been introduced. On little dry mounds in the middle of ponds we again found *Cirsium acaulon* and much *Spiranthes spiralis*. The pits also produced *Samolus valerandi*, *Serratula tinctoria*, *Ranunculus lingua*, *Trifolium fragiferum* and *Typha angustifolia*.

The meeting formally ended after the comparative study of these four habitats; but some members, not glutted by seeing all the above and other species too numerous to mention, drove on to a nearby village pond containing masses of *Illecebrum verticillatum* and some *Mentha pulegium*. The riches of The New Forest area had been abundantly enjoyed.

J. OUNSTED

PUTNEY TO KEW, SURREY. 4TH SEPTEMBER

A large party of members and friends gathered on the Surrey side of Putney Bridge for a perambulation of the Thames towpath from Putney to Kew. With only the exception of the stretch between the bridges at Barnes and Chiswick, the day was spent on the Surrey bank. This stretch of the river holds the remnants of Surrey's formerly richer and more extensive maritime flora. There are single plants of *Triglochin maritima* and *Carex divisa* on the embankment between Putney and Hammersmith, a solitary *Aster tripolium* just upstream of Hammersmith Bridge, where it has a long recorded history, and several patches of *Scirpus maritimus*, notably at Kew, but also on the Putney-Hammersmith stretch.

The towpath is surprisingly rich in a mixture of native, naturalized and planted trees. Poplars are especially well represented. The meeting was able to compare *Populus nigra* (mostly old trees of both sexes on the embankment wall), *P.* × *canadensis* (present as at least two clones, the male 'Serotina' and the female 'Regenerata'), *P. alba* (including the erect-branched 'Fastigiata', which was coming true from its suckers) and fastigiate black poplars, which mostly seem to be a female clone of 'Plantierensis', a more vigorous tree than the male 'Italica' to which the name Lombardy Poplar truly belongs. Amongst the other exotic woody flora were a large *Ficus carica*, in fine fruit downstream from Hammersmith Bridge, *Morus nigra* just below Chiswick Bridge and *Ligustrum ovalifolium* upstream from Hammersmith. There were opportunities to observe the variation encompassed by *Ulmus procera*, *U. glabra* and *U.* × *hollandica*, whilst on the Middlesex bank at Barnes the two bushes of *Salix daphnoides* were admired. These *Salix* bushes are given in error as plants of the Surrey bank in Lousley's *Flora of Surrey*. Below the railway bridge at Kew, a large bush of a green-fruited Elder, *Sambucus nigra* f. *viridis*, caused much comment; this form also occurs on other parts of the towpath.

Of interest among the herbaceous flora is the commonest dock of the area, the alien *Rumex obtusifolius* subsp. *transiens*, which has been recorded from here for over a century. Another patch of alien docks at Barnes caused some consternation as the plants seemed to range from *R. patientia* to *R. cristatus* and back again. Several plants of the native *Polygonum mite* were discovered growing with *P. hydropiper* on the river wall at Kew. Excursions into the tricky world of michaelmas daisies produced *Aster novi-belgii* and *A.* × *salignus*, but *A.* × *versicolor* and *A. lanceolatus* are also known to occur. The aliens *Angelica archangelica* and *Bromus carinatus* are characteristic features of this part of the Thames. Other notable aliens recorded along the towpath during the day were *Hirschfeldia incana*, *Rorippa austriaca*, *Bunias orientalis* and the pretty, pink-flowered *Calystegia pulchra*.

The meeting ended by the church on Kew Green, in whose yard *Sisymbrium strictissimum*, *Phytolacca esculenta*, *Sisyrinchium striatum* and *Gnaphalium* cf. *purpureum* are established. The more adventurous returned to Putney by boat, others lingered in the church, once it was discovered that the good ladies of Kew serve a splendid tea there on a Sunday afternoon!

A. C. LESLIE

WALES

LYDART, MONMOUTH. 9TH–10TH JULY

This meeting was held in association with the Welsh A.G.M. Saturday morning was spent walking through Caer-Llan Woods, Glanau Wood and Atkins Hill Wood to see, in particular, a slope covered with *Gymnocarpium dryopteris* in a wood carpeted with *Corydalis claviculata*. As this was a happy hunting ground for Rev. Augustin Ley and Rev. W. H. Purchas, co-authors of the 1889 *Flora of Herefordshire*, a large number of brambles were identified by Alan Newton, including the two named after the two vicars. The party was then taken up a lane to where *Gaultheria shallon* and *Cicerbita macrophylla* grew side by side.

The Sunday meeting began at the Pecket Stone car park with *Corydalis claviculata* again abundant in the acid woodland. Attention was then turned to Cleddon Bog, an area of mainly common land, to see the remnant of what was previously a species-rich bog. *Narthecium ossifragum*, *Eriophorum angustifolium* and *E. vaginatum* were very noticeable among the *Calluna vulgaris* and *Erica tetralix*, while *Drosera rotundifolia*, *Vaccinium oxycoccus* and *Dryopteris carthusiana* had to be searched for. Next a road verge, rich in such species as *Dactylorhiza maculata* subsp. *ericetorum*, *D. fuchsii* and *Listera ovata*, was compared with the other verges around the bog. On the latter verges hogweed had crowded out most other species after a farmer had discharged his slurry on the verges.

The next brief stop was at the side of a woodland brook at Llandogo. Here *Stellaria nemorum* intermediate between subsp. *glochidispermum* and subsp. *nemorum* occurred in two large patches, with their large white flowers having divided petals curved backwards, so typical of this species. A climb then took the party up to a woodland path, where *Lilium martagon* was flowering on stems 2 m high. *Luzula forsteri* and *L.* × *borreri* were passed on the way and another site of *Stellaria nemorum* was observed on a wooded stream bank. This was the only incursion into England. A quarry floor at Blackcliff had so little soil on it, that as yet no density of vegetation has crowded out the large numbers of *Euphorbia serratula* that have flourished there for many years. *Monotropa hypopitys* flowered nearby. A green cathedral formed by beech trees overhead, and with such ferns as *Dryopteris filix-mas*, *D. austriaca*, *D. affinis*, *Polystichum setiferum*, *P. aculeatum* and *Athyrium filix-femina* beneath, was the home of *Chrysosplenium alternifolium*. Other species seen were *Carex strigosa*, *Hieracium stenstroemii* and *Epipactis helleborine*.

The last site in the Wye Valley was a remnant of a brookside marsh which once filled a mile of the valley, now a leased reserve of the Gwent Trust for Nature Conservation. Though very small it contained *Pedicularis palustris*, *Anagallis tenella*, *Triglochin palustris*, *Senecio aquatilis*, *Potamogeton polygonifolius*, *Dactylorhiza fuchsii*, *D. maculata* subsp. *ericetorum*, *D. praetermissa*, *Valeriana dioica*, *Menyanthes trifoliata* and the sedges *Carex pulicaris*, *C. echinata*, *C. nigra*, *C. paniculata*, *C. hostiana*, *C. laevigata*, *C. panicea*, *C. flacca* and *C. acutiformis*. *Aconitum napellus* bordered the brook inside and outside the reserve.

T. G. EVANS

CWM LLYFNANT, CARDIGANSHIRE. 31ST JULY

Forty six members and friends met at Glaspwll to spend the last day of the hot weather in the Cwn Llyfnant S.S.S.I. Walking down the road on the Cardiganshire side of the stream we saw locally uncommon species such as *Milium effusum*, *Lamiastrum galeobdolon*, *Mycelis muralis* and a great abundance of *Hymenophyllum wilsonii* on the wet, wooded slopes wherever slightly base-rich rocks outcropped. *Tilia cordata* and *Ulmus glabra* were conspicuous in what remained of the native woodland of the valley. We made a difficult descent through fallen oaks and willows (casualties, like much of the conifer forest in the valley, of the hurricane of 13th December 1981) and inspected, from stable ground, a large but precarious colony of *Stellaria nemorum* subsp. *glochidisperma* on a moss-covered scree. After lunch we had an even steeper climb, above the road, examining subspecies of *Dryopteris affinis*, flushes with *Carex laevigata*, and deep *Calluna* and *Sphagnum* on 60° slopes. The more agile members reached a massive boulder scree at 240 m, and saw *Hymenophyllum tunbrigense* deep down in the hollows, the only site in the county where it occupies this habitat that is so characteristic for it in Snowdonia. At the back of a cave we saw a fine display of the protonemal mass of the moss *Schistostega* reflecting an emerald green glow. Thanks are due to the Economic Forestry Group and to the Allt-ddu estate for permission for parking and access.

A. O. CHATER

SCOTLAND

BALERNO, LOTHIAN. 21ST MAY

This joint meeting with the Botanical Society of Edinburgh had two main aims: first to introduce field botany to some 'beginners' in the B.S.E. 'Botany of the Lothians' flora project and mapping scheme, and second to test the new 1983 recording sheets and scheme for the said survey. Both aims were achieved – habitat recognition as well as plant recognition were well-rehearsed. 22 people attended.

The area chosen, around the Marchbank Hotel, Balerno, is physiographically delightful and contains many different habitats – streams, a lake, several woodland types, amenity ground, various farmland habitats, ruderal areas and a splendid marsh. Most of the vegetation is of common plants, typical of their habitats, forming a good basis for elementary introduction. The diet was not too rich for beginners and yet – in critical willows, birches, and planted conifers, as well as vegetative material (a late season) – provided a test for the experienced. Much attention was paid to demonstrating species of grasses, rushes and sedges, and the family differences were well seen.

After an enjoyable luncheon, the party moved on to the profuse riverbank flora of the Water of Leith below Balerno Bridge in a session less formal than the forenoon's. Early splashes of colour from *Montia sibirica*, the comfreys and *Doronicum* (rampaging everywhere now) would soon be replaced by gaudy *Mimuli*. Tall stems of *Phalaris arundinacea* (shortly to be outclassed by *Bromus ramosus*) delighted the eye, while dense stands of *Allium ursinum* and *A. paradoxum* exercised the nostrils. *Arum maculatum*, reduced to rarity only a little to the north, now flourishes below the late Dr J. W. Gregor's house: how our much-missed colleague would have admired it!

P. M. SMITH

BALLINLUIG, PERTHSHIRE. 5TH JUNE

This excursion, part of the first B.S.B.I. Scottish Recorders' Conference, was also joint with the Perthshire Society of Natural Science, Botanical Section. As a result, an impressive array of 19 v.c. Recorders plus 14 other members and friends of both Societies attended. The weather blessed us with only the second sunny afternoon in months and everyone enjoyed a delightful afternoon's botanizing amongst carpets of *Primula veris* beside the River Tummel. Such pleasures apart, the aim of the excursion was to add to the rather scant previous records for Tomdachoille 'Island', a shingle bank deposited by the River Tummel since c. early 19th century and now partly joined to the 'mainland' (much to the relief of some excursion members!). Its relationship to the river channel at various dates caused (and is still causing) debate as to its v.c. allegiance but this did not dampen the enthusiasm of recorders.

The Perthshire shingle islands are characterized by a wide variety of habitats and consequent species diversity. Tomdachoille was no exception, a total of 368 species (including previous records) now being recorded in habitats ranging from unimproved grassland to woodland, open shingle, backwater and flushes. The most interesting finds were *Primula veris* × *vulgaris*, *Neottia nidus-avis*, *Equisetum pratense*, *Melica nutans*, *Ranunculus auricomus*, *Rubus saxatilis* in the woodland, *Saxifraga granulata*, *Helictotrichon pubescens*, *Vicia sylvatica*, *Potentilla anglica*, *Ranunculus bulbosus* in the grassland, and *Draba incana* and *Filago minima* on the more open shingle and sand deposits.

Our thanks are due to the owner, The Duke of Atholl, for permission to visit the area, and to Mr Stewart for kindly tolerating so many cars littering his farm.

R. A. H. SMITH

CAMPSIE HILLS, STIRLINGSHIRE. 18TH JUNE

The venue chosen was Fin Glen, near Lennoxtown, a steep-sided glen running north into the basalts of the Campsie Hills, and the meeting, which was held jointly with the Glasgow Natural History Society, was attended by nine persons. The weather proved exceptionally fine.

The route lay parallel to the west bank of the Fin Burn, and progress was fairly rapid in an effort to reach the upper parts of the glen without undue delay. In the open hill pasture *Viola lutea* was frequent, occurring in several colour forms ranging from yellow to purple. On reaching a point above the limit of woodland we descended to the stream-side and continued upstream at a more leisurely pace, examining the flora of the rock outcrops. The more noteworthy plants seen here were *Cystopteris fragilis*, *Geranium lucidum*, *Saxifraga hypnoides*, *S. aizoides*, *Melica uniflora* and *Helictotrichon pubescens*. The lower wooded portion of the glen, being steep-sided, boggy in places, and therefore rather difficult of access, was nevertheless tackled by the more active members of the party. At a prominent waterfall *Asplenium viride* was seen in some quantity, but *Paris quadrifolia*, reported many years ago from this locality, was not re-discovered, although the habitat seemed eminently suitable.

A. McG. STIRLING

CAM CHREAG, BRIDGE OF ORCHY. 25TH JUNE

Thirty two members of the B.S.B.I. and B.S.E. (Alpine section) and their friends assembled by courtesy of Lord Trevor near the viaduct at Auch and set off along a flat-bottomed glen to ascend the wall-like side of Cam Chreag's north west ridge. This ridge and Cam Chreag's northern ridge delimit the extent of v.c. 98 here, and in this area 101 species of vascular plant were seen by the 'slow' party before they penetrated into the main part of the hill which is in v.c. 88. Meanwhile a larger party hurried on to v.c. 88 and made a study of the west and south sides of the hill, returning rapidly via the east side in deteriorating weather conditions. The sunny south-western side and south-eastern corner produced the most interesting plants including *Bartsia alpina*, *Dryas octopetala* and *Woodsia alpina*, the last it seems for the first time on this hill. The wetter and shadier north-eastern cliffs featured two colonies of *Cystopteris montana*. Altogether 150 species of vascular plant were seen.

For its height (880 m) Cam Chreag is an exceptionally rich hill for montane plants both in numbers of species and quantity of the more interesting ones. *Cherleria sedoides*, *Cerastium alpinum* and *Polygonum viviparum* in particular were very abundant and have been so on each of my four visits to the hill. Other species appear to vary in abundance. 1983 seems to have been a bumper year for *Adoxa moschatellina*, *Carex vaginata* and *Juncus triglumis*. *Ranunculus auricomus* also was more noticeable this year. 64 species were seen in v.c. 88 which were not in v.c. 98. These included *Potentilla crantzii*, *Salix reticulata* and other arctic-alpines and some wetland species. 16 species seen in v.c. 98 but not in v.c. 88 included *Salix lapponum* and *Salix phylicifolia* but were mainly of more lowland types.

The somewhat bedraggled party on return were very appreciative of the 'cup of tea' generously provided by Lady Trevor.

A. A. P. SLACK

LAUDERDALE AND COCKBURNSPATH, BERWICKSHIRE. 2ND–3RD JULY

A sunny walk in the Lammermuirs was enjoyed by nine members on the Saturday. Up Soonhope Burn, *Helianthemum chamaecistus* and *Veronica officinalis* were seen in spectacular profusion, and *Gymnocarpium dryopteris* was an unexpected find on scree. *Sedum villosum* was locally plentiful near the burn. Crossing to Whalplaw Burn, a *Carex disticha* flush added *Valeriana dioica* but no orchids. However, three cleuchs were penetrated to advantage. Thorneycleuch and Gladescleuch carry extensive tall juniper scrub which extends also down the main burn. Foxes Cleuch has a profusion of ferns with *Lycopodium clavatum* and a large patch of *Gymnocarpium dryopteris* together with *Geranium sylvaticum* and *Salix aurita*. By the main burn *Sedum villosum* was again present and *Hieracium anglicum* by a rocky linn.

Dunglass Dean, on the border between v.c. 81 and v.c. 82, attracted 13 members on the Sunday, and the majority of the party braved the rocky bed of the burn below impressive sandstone cliffs shaded by oak and as yet healthy elm. *Carex pendula* was frequent with *Eupatorium cannabinum*, *Equisetum telemateia* and naturalized *Fuchsia magellanica*. *Chrysosplenium alternifolium* was occasional but old records for both *Melica* species were not refound. In Bilsdean *Symphytum asperum* was admired near a spectacular linn. On the shore *Atriplex littoralis* and *Cakile maritima* were seen. A sandy area yielded *Anthriscus caucalis* amongst *Hippophae rhamnoides*, at its northern native limit with the fungus *Phelinus hippophaecola*, also seen were *Cerastium semidecandrum* and *Catapodium rigidum*, these species are restricted to v.c. 82. The gateway to an arable field yielded *Trifolium striatum* and *Lamium amplexicaule*. By the roadside *Humulus lupulus* with the leaves unlobed was noted. Sadly none of the nine choice nineteenth century records selected for attention had been refound.

M. E. BRAITHWAITE

TOMINTOUL, BANFFSHIRE. 5TH–10TH JULY

The purpose of this meeting was to record under-worked areas of Banffshire, v.c. 94, for a proposed check list. Over 40 members and friends attended, which together with the brilliant sunshine that lasted all week, enabled a far greater area to be covered than had been anticipated. Recording was based on 5 km grid squares; in total 18 squares were visited and 3,258 species recorded, which included 259 new 10 km square and 1,056 new 5 km square records. The group was divided into four parties on most days.

On the first day the Cromdale Hills were visited, an area mainly covered by heather moor, which is much burned and sheep-grazed. Two members climbed Craggan a'Chaise (2367 ft) from Bridge of Brown, by way of the March Burn. An abundance of *Rubus chamaemorus*, *Genista anglica*, *Trientalis europaea* and a small quantity of *Saxifraga stellaris* were seen. Others kept to the lower ground in square 38/12 S.W., working up the Lochy Burn from Inverlochy. Two unexpected N.C.R.s were found in a farm yard: *Amsinckia intermedia* and *Poa palustris*. In square 38/12 N.W. similar terrain was covered but with the addition of the banks of the River Avon. Half the species seen were in this latter habitat, the most interesting being *Cardaminopsis petraea*, washed down from the hills, and *Peplis portula* found by an old mill pool. In square 38/13 S.E., birch woods of Kilnmaichie and banks of the River Avon were visited. The best find of the week, *Arctostaphylos alpinus*, was recorded on broken ground near the summit of Creag an Tarmachain. One species-rich bog was encountered where occurred *Parnassia palustris* and another bog had *Myrica gale*, a plant not common in the county. In square 38/13 N.E., the policies of Ballindalloch Castle were visited. Many of the species were introductions such as *Tellima grandiflora*, *Euphorbia dulcis*, *Cotula squalida* and *Carex pendula*. On consolidated shingle occurred *Arabis hirsuta*, *Cardaminopsis petraea*, *Helianthemum nummularium*, *Lupinus nootkatensis* and *Galium sterneri*.

On the second day two parties proceeded to Blackwater Lodge by way of Glenfiddich Lodge, where a stop was made to photograph a large herd of deer. In square 38/32 S.W., blanket bog and moorland on the north side of the Ladder Hills and outcrops of serpentine rock by the Black Water Burn were visited. These outcrops were of interest, an abundance of *Silene vulgaris* subsp. *maritima*, *Cochlearia officinalis*, *Minuartia verna*, *Armeria maritima* and *Anthyllis vulneraria* and the two ferns *Asplenium viride* and *A. cuneifolium* were present. *Lycopodium annotinum* was common on the moorland. In square 38/32 N.W. moorland, river and one very dry serpentine outcrop at Blackwater Lodge were visited. Near the lodge were *Vaccinium microcarpum*, *Sedum villosum* and *Glyceria declinata*. The high ground had *Chamaepericlymenum suecicum*, *Rubus chamaemorus*, *Saxifraga stellaris* and by a snow patch some *Loiseleuria procumbens* in flower. In square 38/22 N.E., Glen Suie and Carn an t'Suidhe were visited. The area was of low botanical interest except for a few good flushes by the confluence of the Black and Fore Burns. Here were recorded *Epilobium alsinifolium*, *Equisetum sylvaticum* and *Cirsium helenioides*. In square 38/22 S.E., Glen Livet, River Livet and Black Burn were visited. On the drier ground occurred *Viola lutea*, *Antennaria dioica*, *Botrychium lunaria*, *Coeloglossum viride* and *Carex caryophyllea*. *Sedum villosum* and *Carex pauciflora* were found locally.

On the third day in square 38/23 N.E., Meikle Conval (1867 ft) was visited, it had patches of *Genista anglica* and *Arctostaphylos uva-ursi*, and a sheltered bank had a small colony of *Pyrola media*. Ben Rinnes (2,755 ft) had the addition of *Rubus chamaemorus*, and at its summit *Lycopodiella alpina*, *Lycopodium annotinum*, *Solidago virgaurea*, *Loiseleuria procumbens* and *Luzula spicata*. One good flush on the east side of the summit had *Sibbaldia procumbens* in some quantity and *Epilobium anagallidifolium*. In square 38/23 N.W., the northern face of Ben Rinnes was visited. A small quantity of *Sibbaldia procumbens* was seen near Scurran of Morinsh.In square 38/23 S.W. moorland at Morinsh on the south-western side of Ben Rinnes and banks of the Tervie Burn at Milltown of Tombreckachie were visited. The best find was *Caltha palustris* subsp. *minor* in a runnel on the Ben. The Tervie Burn was rich in species including *Trollius europaeus* and the beautiful petaloid form of *Mimulus cupreus* × *M. guttatus*. In square 38/23 S.E., Achbreck, Thunderlap Hill and Corriehabbie Burn were visited. Many sedges were found, also *Viola lutea*, *Rumex sanguineus* subsp. *viride*, *Salix pentandra* and *Lamium album*.

The next day was 'free' and most of the party went down to Inchrory Lodge. Two squares in Glen Avon were recorded (38/11 S.W. and S.E.). Allt Bheithachan and Wester Gaulrig were visited. A calcareous bank yielded a new locality for *Carex capillaris*. Meikle Fergie Burn proved to be a very rich area. Here were found *Dactylorhiza fuchsii*, *D. purpurella* and their hybrids, *Glyceria declinata*, *Viola lutea*, *Ranunculus bulbosus*, *Helianthemum nummularium*, *Meum athamanticum*, *Listera ovata* and *Carex caryophyllea*. A gorge in the burn had *Pyrola minor*, *Carex sylvatica*, *Festuca gigantea* and *Melica nutans*.

On the fifth day Glen Avon was again visited. In square 38/10 S.W., the Lochan nan Gabhar area produced the expected artic-alpines. In square 38/10 S.E., Allt Gaineimh was visited, although this square already had a very large number of records, additions of great value were made, including *Loiseleuria procumbens*, *Gnaphalium supinum* and *Juncus trifidus*. In Upper Glen Avon (square 38/10 S.E.) *Betula nana* and *Hieracium hanburyi* were found on the south side of the river. Upstream from Bridge of Loin a few base rich flushes had a good *Carex* flora and drier slopes produced *Gymnadenia conopsea*, *Polygonum viviparum*, *Lathyrus montanus* var. *tenuifolius*, *Vicia sepium* and *Potentilla erecta* subsp. *strictissima*. In square 38/00 N.E. the party ascended to an apparent lochan, but it proved to be a large hollow in a peat-bog complex, dry and devoid of plants. The associated ridges and nearby hills had a poor moorland flora and poor summit floras on their granite outcrops. Cnap an Dobhrain had *Loiseleuria procumbens*, *Carex pauciflora* and locally abundant was *Vaccinium uliginosum*. On the south side of the river was found *Cystopteris fragilis* and *Betula nana*.

On the last day a depleted party visited the Culbin State Forest and so ended a most useful week's mapping. Grateful thanks are given to all the members of the party, especially the sub-leaders, Catriona Murray, Olga Stewart, Michael Braithwaite and George Forster. Thanks are also due to those who identified plants, especially Alan Silverside, to the many landowners, keepers and farmers who allowed us to invade their land and to the Richmond Arms Hotel for the facilities provided during our stay.

M. McC. Webster

GOLSPIE, EAST SUTHERLAND. 11TH–15TH JULY

The meeting, held jointly with the B.S.E., was based at Golspie and covered eastern parts of v.c. 107. Ten members and a varying number of local non-members took part. Monday dawned dull but cleared fast on the high ground to roast the party investigating Ben Horn and its loch. The loch was dull, the hill a little better with *Salix herbacea*, *Arctostaphylos alpinus* and *Chamaepericlymenum suecicum*. Meanwhile a second party worked northwards along the coast over the limestone outcrop of Uppat to the beautiful shoreline waterfall at Doll. *Asplenium marinum* was plentiful despite being declared extinct in the 'Flora'. There was abundant *Astragalus danicus* and *Botrychium lunaria*. *Lupinus polyphyllus* was new and *Dryopteris carthusiana* was a second v.c. record.

On Tuesday most people avoided the worst of the heat; one group investigated the seashore turf and dune links of Dornoch Point, in a square on the county boundary and not much surveyed on the Sutherland side. Consequently 115 new square records were added including *Genista anglica* and *Sorbus intermedia* as second v.c. records and *Papaver argemone* and *Lathyrus latifolius* as first records. The second group explored the margins of Loch Evelix with some river and seashore. Here new v.c. records were *Sparganium emersum*, *Centranthus ruber* and *Callitriche hermaphroditicum*, and there were 22 new square records.

Wednesday was spent round the headwaters of the Evelix River, including Loch an Lagain. One party examined the craggy boulder outcrops of Craig a' Ghobhair and the loch below, the tedium of barren crags and barren loch being broken only by counting one's cleg bites! The second party fared better with base-rich mires around their loch and after a sequence of barren crags the late reward of a single outcrop having *Helianthemum chamaecistus*, *Ajuga pyramidalis* and typical associates. 24 new square records were added including the results of some general square-bashing by one member.

Next morning the rich undergrowth of Balblair Wood revealed its gems. *Moneses uniflora*, *Linnaea borealis* and *Goodyera repens* were in perfect flowering condition and new to several members. The afternoon was spent on the large Craig an Amalaidh by Cambusmore where the upper crags proved tempting but inaccessible while the lower ones yielded *Polystichum lonchitis*, *Viburnum opulus* and *Sorbus rupicola*.

Only two members had seen *Ajuga pyramidalis* during the week and it was going to be a first for several members: it had to be found before mid-day so the whole party combed tangles of bracken and gorse around the Mound Rock until a parched colony, long past flowering, was located. Off then to Silver Rock where the crags were dull except for two patches–one having abundant *A. pyramidalis*, the other having also *Helianthemum chamaecistus*, *Cystopteris fragilis* and other associates. The party dispersed having delivered 200 new square records plus at least 12 publishable v.c. records.

J. K. BUTLER

KINDROGAN, PERTHSHIRE. 27TH JULY–3RD AUGUST

The course, held at Kindrogan Field Centre, was designed to cater for beginners and advanced students alike. It was attended by 16 people including three B.S.B.I. members. On the first evening Mr Brian Brookes, the Warden, gave a lecture on types of inflorescence and methods of describing flowers. This was followed by a tour of Kindrogan's grounds during which the main plant families were described and illustrated by specimens found on the walk. Progress was so rapid that the latter part of the walk was much concerned with identification of various willows and their hybrids.

Ailsa Lee relieved Mr Brookes on the 29th, and took the students to the Tummel at Pitlochry, the roadside verges and woodland at Logierait, and the dry shingle beds of the Tummel at Ballinluig. At Logierait were *Leonurus cardiaca* and *Chrysanthemum segetum*.

On the following day the sites visited were the Birks of Aberfeldy and Brerachan Meadow. The latter is now dominated by *Filipendula ulmaria*, but *Geranium sylvaticum* is still common, and *Meum athamanticum* survives. At Aberfeldy were *Asplenium viride*, *Vicia sylvatica* and *Stellaria nemorum* as well as several ferns, sedges and grasses of interest.

Tomphubil and the limestone areas near Schiehallion were visited for the rich flora local to these sites, including *Gentianella amarella*, *Gentianella campestris*, *Astragalus danicus* and *Convallaria majalis*, while Lochan an Daim was fringed with *Carex lasiocarpa* and *Phragmites communis*. At Loch Kinnardochy, the group was introduced to aquatic, semi-aquatic and marsh plants, particularly *Potentilla palustris*, *Lobelia dortmanna* and *Littorella uniflora*.

For arctic/alpine plants the group visited upper Glenshee, and found a number of interesting plants in the relatively base-rich soil. At two sites in Glenshee *Polystichum lonchitis* and *Oxyria digyna* were recorded, the former in a roadside quarry, the latter on riverine shingle beds.

The fieldwork concluded with a very successful visit to the nature reserve at St Cyrus, where saltmarsh, strandline, consolidated dunes and base-rich cliff habitats introduced the group to several species, including *Astragalus glycyphyllos*, *Honkenya peploides*, *Campanula glomerata*, *Juncus gerardii* and *Dianthus deltoides*. The culmination of the week's excursions and study was an exhibition attended by many members of the local community.

D. ADAMSON

IRELAND

LOCH ENNEL, WESTMEATH. 18TH JUNE

This meeting was planned as an educational outing, but unfortunately was very poorly attended. Species rich grassland and fen were examined and *Carex appropinquata* was seen in considerable quantity in nearby meadows.

D. DOOGUE

MOURNE MOUNTAINS, CO. DOWN. 30TH–31ST JULY

Eight members and friends attended this meeting. On the Saturday they ascended the Glen River from Newcastle to visit the site of *Asplenium trichomanes* subsp. *trichomanes* on Thomas's Mountain. This was duly located, and the party then proceeded to examine the plants on slate outcroppings at c.1500 ft. The most interesting plants found were Beech Fern and a *Hieracium*, probably *H. hypochoeroides*. *Saxifraga stellaris* was noted in a nearby flush.

On the Sunday the party visited an escarpment, with outcroppings of Silurian slate rock at c.1800 ft, on Slieve Muck to examine alpine plants. *Saussurea alpina* has been recorded from here, but was not located on this occasion. Parsley Fern, Beech Fern, *Lycopodium alpinum*, *Vaccinium vitis-idaea* and *Sedum rosea* were all seen. *Hieracium ?hypochoeroides* was found again; this will be a new v.c. record if it has been correctly identified. The party then proceeded across the valley to the Pigeon Rock, where there are similar outcrops of rock, but despite old records of a similar flora to that of Slieve Muck nothing of interest was found there.

P. HACKNEY

GLENASMOLE, CO. DUBLIN. 28TH AUGUST

The outing to Glenasmole and Bohernabreena was most successful, with a dozen members and friends attending. Most of the aquatic and shore-line species from the waterworks at the upper lake were rediscovered (including *Potamogeton perfoliatus*, *Ranunculus aquatilis* and *R. trichophyllus*), and two species of *Hieracium* were collected for further examination. Attempts to refind *Monotropa hypopitys* and *Hammarbya paludosa* were unsuccessful, but this failure may be due in part to the exceptionally dry summer.

R. MCMULLAN

FIELD MEETING, 1982 (ADDITIONAL REPORT)

THE COTSWOLDS, GLOUCESTERSHIRE & OXFORDSHIRE, 4TH & 5TH JULY

Fourteen members assembled near Painswick Beacon on the Saturday and, before proceeding to the downland, were shown *Rubus balfourianus*, *Geranium endressii* and *Symphytum* × *uplandicum* growing on the road verges.

The orchid banks on the slopes below Painswick Beacon, Common Land, are severely threatened by the rapid encroachment of *Pinus nigra*; members helped the conservation ideal by (very discreetly!) removing 50 or more seedlings of this troublesome conifer. Numerous orchid species were seen here including a fine display of *Herminium monorchis*; below it *Astrantia major* was marked by road-side reserve posts in a long established site. *Asperula cynanchica*, *Hippocrepis comosa* and *Astragalus danicus* were noteworthy among the rich flora of the Oolite. In a nearby beechwood the party had a fine opportunity of comparing *Bromus ramosus* and *B. benekenii* and saw *Monotropa hypopitys*. *Campanula poscharskyana* was noted nearby under a wall.

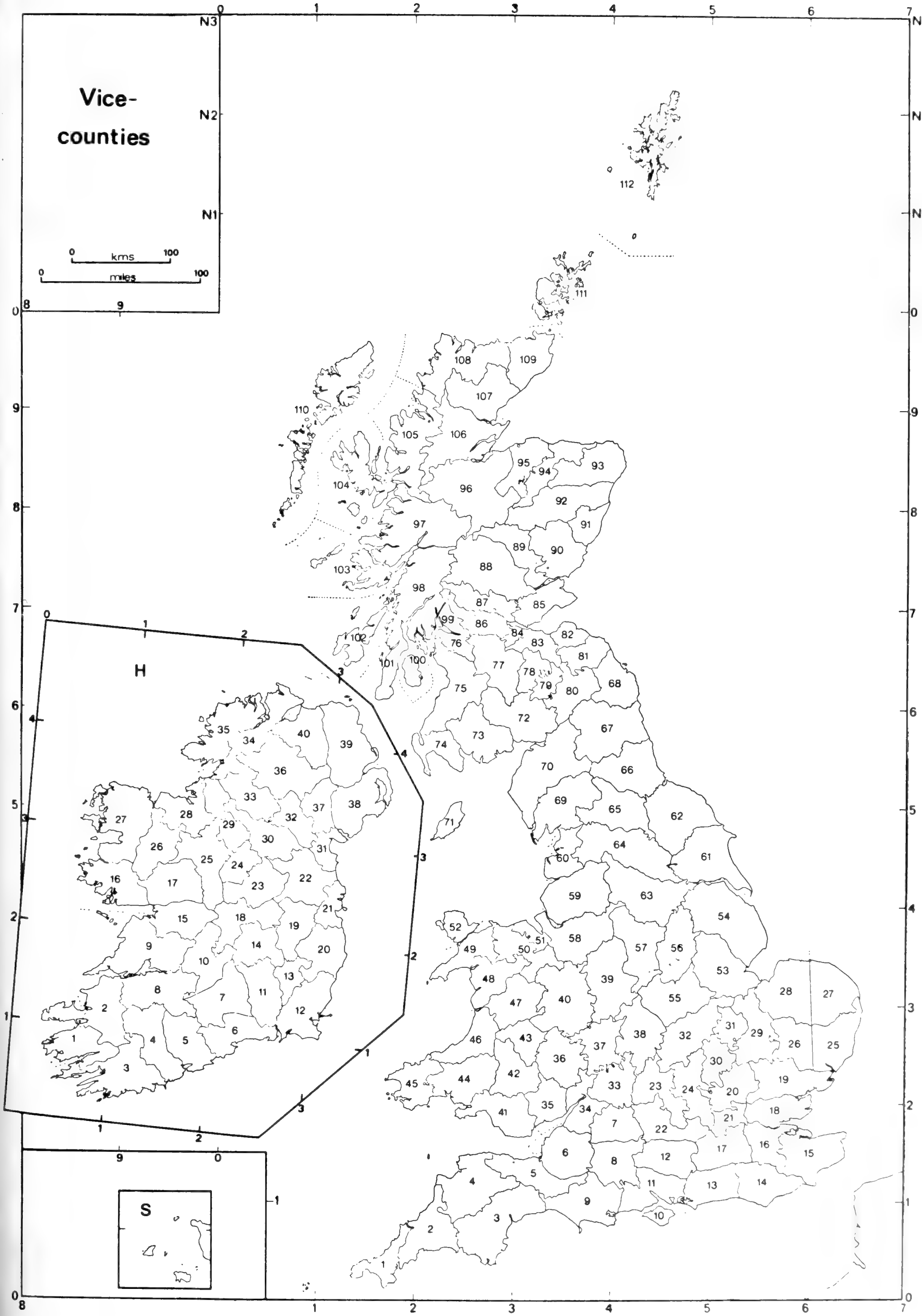
The afternoon session opened in a small wood on Scottsquar Hill where *Geranium nodosum*, *Helleborus orientalis*, *Hepatica nobilis* and *Vinca minor* are well established. The downland itself, a well-known beauty spot somewhat threatened by public access and motorcyclists, affords excellent panoramic views and the Malverns and the Welsh mountains were easily visible. The flora is again rich in orchid species and is typical of the Cotswold grasslands. Interlopers noted included *Lonicera nitida* and *Mahonia aquifolium*. A wealth of interesting species was examined in the disused quarry including an as yet unidentified *Dianthus* sp., *Rosa rugosa*, *Syringa vulgaris* and the natives *Galeopsis angustifolia* and *Vicia sylvatica*.

Most of the party continued to Stow-on-the-Wold for overnight accommodation and evening meal. The welcome repast was followed by a short slide show and discussion which took place in a delightful upper room kindly made available to us by the owner of the Gemini Restaurant.

Having seen prime examples of limestone grassland habitats the previous day, members on the Sunday were asked to contribute to the knowledge of lesser known sites, mostly in Oxfordshire and to provide up to date information on the populations of three nationally rare species, *Salvia pratensis*, *Stachys germanica* and *Thlaspi perfoliatum*. The centre of distribution for these species is the Gloucestershire/Oxfordshire borders. In all five groups visited about a dozen sites and provided species lists and population forms.

At the end of the day members met again in Stow, over a cream tea, and pooled information including observations on cornfield weeds, e.g. *Kickxia* spp., *Legousia hybrida* and *Chaenorhinum minus*, a delightful additional interest to the Cotswold flora.

A. L. GRENFELL & J. MARTIN



Vice-counties

NAMES OF VICE-COUNTIES IN *WATSONIA*

ENGLAND, WALES AND SCOTLAND

1. W. Cornwall
1b. Scilly
2. E. Cornwall
3. S. Devon
4. N. Devon
5. S. Somerset
6. N. Somerset
7. N. Wilts.
8. S. Wilts.
9. Dorset
10. Wight
11. S. Hants.
12. N. Hants.
13. W. Sussex
14. E. Sussex
15. E. Kent
16. W. Kent
17. Surrey
18. S. Essex
19. N. Essex
20. Herts.
21. Middlesex
22. Berks.
23. Oxon
24. Bucks.
25. E. Suffolk
26. W. Suffolk
27. E. Norfolk
28. W. Norfolk
29. Cambs.
30. Beds.
31. Hunts.
32. Northants.
33. E. Gloucs.
34. W. Gloucs.
35. Mons.
36. Herefs.
37. Worcs.
38. Warks.
39. Staffs.
40. Salop
41. Glam.
42. Brecs.
43. Rads.
44. Carms.
45. Pembs.
46. Cards.
47. Monts.
48. Merioneth
49. Caerns.
50. Denbs.
51. Flints.
52. Anglesey
53. S. Lincs.
54. N. Lincs.
55. Leics.
55b. Rutland
56. Notts.
57. Derbys.
58. Cheshire
59. S. Lancs.
60. W. Lancs.
61. S.E. Yorks.
62. N.E. Yorks.
63. S.W. Yorks.
64. Mid-W. Yorks.
65. N.W. Yorks.
66. Co. Durham
67. S. Northumb.
68. Cheviot
69. Westmorland
69b. Furness
70. Cumberland
71. Man
72. Dumfriess.
73. Kirkcudbrights.
74. Wigtowns.
75. Ayrs.
76. Renfrews.
77. Lanarks.
78. Peebless.
79. Selkirks.
80. Roxburghs.
81. Berwicks.
82. E. Lothian
83. Midlothian
84. W. Lothian
85. Fife
86. Stirlings.
87. W. Perth
88. Mid Perth
89. E. Perth
90. Angus
91. Kincardines.
92. S. Aberdeen
93. N. Aberdeen
94. Banffs.
95. Moray
96. Easterness
96b. Nairns.
97. Westerness
98. Main Argyll
99. Dunbarton
100. Clyde Is.
101. Kintyre
102. S. Ebudes
103. Mid Ebudes
104. N. Ebudes
105. W. Ross
106. E. Ross
107. E. Sutherland
108. W. Sutherland
109. Caithness
110. Outer Hebrides
111. Orkney
112. Shetland

IRELAND

H1. S. Kerry
H2. N. Kerry
H3. W. Cork
H4. Mid Cork
H5. E. Cork
H6. Co. Waterford
H7. S. Tipperary
H8. Co. Limerick
H9. Co. Clare
H10. N. Tipperary
H11. Co. Kilkenny
H12. Co. Wexford
H13. Co. Carlow
H14. Laois
H15. S.E. Galway
H16. W. Galway
H17. N.E. Galway
H18. Offaly
H19. Co. Kildare
H20. Co. Wicklow
H21. Co. Dublin
H22. Meath
H23. Westmeath
H24. Co. Longford
H25. Co. Roscommon
H26. E. Mayo
H27. W. Mayo
H28. Co. Sligo
H29. Co. Leitrim
H30. Co. Cavan
H31. Co. Louth
H32. Co. Monaghan
H33. Fermanagh
H34. E. Donegal
H35. W. Donegal
H36. Tyrone
H37. Co. Armagh
H38. Co. Down
H39. Co. Antrim
H40. Co. Londonderry

INSTRUCTIONS TO CONTRIBUTORS

Papers and Short Notes concerning the systematics and distribution of British and European vascular plants as well as topics of a more general character are invited.

Manuscripts must be submitted in duplicate, typewritten on one side of the paper only, with wide margins and double-spaced throughout. They should follow recent issues of *Watsonia* in all matters of format, including abstracts, headings, tables, keys, figures, references and appendices. Note particularly use of capitals and italics. *Only underline where italics are required.*

Tables, appendices and captions to figures should be typed on separate sheets and attached at the end of the manuscript. Names of periodicals in the references should be abbreviated as in the *World list of scientific periodicals*, and herbaria as in Kent & Allen's *British and Irish herbaria*. Line drawings should be in Indian ink, preferably on good quality white card, but blue-lined graph paper or tracing paper is acceptable. They should be drawn at least twice the final size and they will normally occupy the full width of the page. Lettering should be done in Lettraset or by high-quality stencilling, though graph axes and other more extensive labelling are best done in pencil and left to the printer. Photographs can be accepted only in exceptional cases.

Contributors are strongly advised to consult the editors before submission in any cases of doubt. Manuscripts will be scrutinized by the editors and a referee and a decision communicated as soon as possible. Authors receive a galley proof for checking, but only errors of typography or fact may be corrected. 25 offprints are given free to authors of papers and Short Notes. Further copies may be purchased in multiples of 25 at the current price.

The Society takes no responsibility for the views expressed by authors of articles.

Papers and Short Notes should be sent to Dr R. J. Gornall, Botany Department, The University, Leicester, LE1 7RH. Books for review should be sent to Dr N. K. B. Robson, Botany Department, British Museum (Natural History), Cromwell Road, London, SW7 5BD. Plant records should be sent to the appropriate vice-county recorders. Reports of field meetings should be sent to Dr B. S. Rushton, Biology Department, The University of Ulster, Coleraine, Co. Londonderry, Ireland.

B.S.B.I. Publications

Special Offer

AN ECOLOGICAL FLORA OF BRECKLAND

by P. J. O. Trist, 1979

210 pages, including 569 distribution maps and ecological notes on 25 Breckland rarities. Also included with the Flora is a transparent overlay showing the locations of the main towns and roads.

The B.S.B.I. has purchased all of the publisher's remaining stock of this book and is now able to offer it to members at the specially reduced price of **£5**, including postage and packing (£5.75, overseas). Orders should be sent with a remittance to the Hon. Treasurer of the B.S.B.I., 68 Outwoods Road, Loughborough, Leicestershire.

Watsonia

February 1985 Volume fifteen Part three

Contents

SHORT NOTES

REPORTS

Published by the Botanical Society of the British Isles

UK ISSN 0043-1532

Filmset by
WILMASET, BIRKENHEAD, MERSEYSIDE
Printed in Great Britain by
EATON PRESS LIMITED, WESTFIELD ROAD, WALLASEY, MERSEYSIDE

WATSONIA

Journal and Proceedings of the Botanical Society of the British Isles

Volume 15 Part 4 July 1985

Editors: J. R. Akeroyd, S. M. Eden,
R. J. Gornall, C. D. Preston,
N. K. B. Robson

ISSN: 0043-1532

Botanical Society of the British Isles

Patron: Her Majesty Queen Elizabeth the Queen Mother

Applications for membership should be addressed to the Hon. General Secretary, c/o Department of Botany, British Museum (Natural History), Cromwell Road, London, SW7 5BD, from whom copies of the Society's Prospectus may be obtained.

Officers for 1985-86

Elected at the Annual General Meeting, 11th May 1985

President, Mr D. E. Allen

Vice-Presidents, Dr N. K. B. Robson, Mr E. C. Wallace, Professor D. A. Webb

Honorary General Secretary, Mrs M. Briggs

Honorary Treasurer, Mr M. Walpole

Back issues of Watsonia are handled by Messrs Wm Dawson & Sons Limited, Cannon House, Folkestone, Kent, to whom orders for all issues prior to Volume 15 part 1 should be sent.

Recent issues (Vol. 15 part 1 onwards) are available from the Hon. Treasurer of the B.S.B.I., 68 Outwoods Road, Loughborough, Leicestershire.

Watsonia, **15**, 309–320 (1985)

Cytology and hybridization in the *Juncus bufonius* L. aggregate in western Europe

T. A. COPE

Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE

and

C. A. STACE

Department of Botany, The University, Leicester, LE1 7RH

ABSTRACT

Chromosome counts in the *Juncus bufonius* L. aggregate (Juncaceae) in Europe are presented. *J. foliosus* Desf. (2n=26), *J. ambiguus* Guss. (2n=34), *J. hybridus* Brot. (2n=34) and *J. sorrentinii* Parl. (2n=28) are considered to be near-diploids, while our concept of *J. bufonius* sensu stricto (incl. *J. minutulus* Krecz. & Gonch.) includes plants at near-tetraploid and hexaploid (and perhaps octoploid) levels. The process of meiosis is described, and the possibility of the existence of diffuse centromeres and inverted meiosis is briefly discussed; the evidence is still equivocal. The results of hybridization experiments between the five segregates of the aggregate are presented. Two hybrid plants were raised from 490 pollinations, both *J. ambiguus* × *J. foliosus*. The plants were more or less intermediate between their parents but totally sterile, with an increased period of flowering and an increased number of flowers per inflorescence unit. Apart from their sterility and floriferousness the hybrids fell within the range of variation of *J. bufonius* sensu stricto.

It is concluded that *J. bufonius* agg. constitutes a polyploid 'pillar' complex, with four diploids in western Europe and a very variable polyploid (*J. bufonius* sensu stricto) at two or three ploidy levels. While the nature of the diploids which originally gave rise to the polyploid complex is not known, it seems likely (judging from the hybridization experiments) that the process is still continuing.

INTRODUCTION

Juncus bufonius agg. belongs to subgenus *Poiophylli* Buch., which comprises annual species with grass-like leaves and a rather diffuse, leafy terminal inflorescence. Also included in the subgenus are *J. tenageia* Ehrh. and *J. sphaerocarpus* Nees, both of which differ from *J. bufonius* agg. in having a spherical rather than oblong capsule. *J. bufonius* agg. is a highly polymorphic group whose morphology has been intensively studied with the result that a number of taxa within it have been recognized at species level. The five species recognized by us in western Europe are (Cope & Stace 1978, 1983): *J. bufonius* L. sensu stricto (incl. *J. minutulus* Krecz. & Gonch.), *J. foliosus* Desf., *J. ambiguus* Guss. (*J. ranarius* Song. & Perr.), *J. hybridus* Brot. and *J. sorrentinii* Parl. These differ in rather critical, but nevertheless constant, ways, mainly on the basis of floral morphology. However, they do share the same weedy habitat and much the same growth form. The inflorescence is of the type technically described as an anthela, but often loosely (and incorrectly) referred to as a panicle. It begins as a dichasial cyme, but after one or two nodes many of the branches become monochasial. Sporadic dichasia may reappear at some of the upper nodes. The internodes between flowers vary considerably in length, and a monochasium may bear from one to six (exceptionally twelve) flowers. Individual plants, especially those that develop into tufts, can remain in flower for a considerable period and seed output is enormous. In the more northerly parts of its range, the flowers of *J. bufonius* agg. are mostly cleistogamous, but there are reports of chasmogamy from warmer latitudes. The evidence, however, is largely anecdotal and to some extent contradictory, so careful observations are still needed (see Laurent (1904) and Shah (1963) for conflicting views).

TABLE 1. PUBLISHED CHROMOSOME COUNTS FOR THE *JUNCUS BUFONIUS* AGGREGATE
J. nastanthus and *J. minutulus* are included by us in *J. bufonius* sensu stricto, and *J. rechingeri* and *J. turkestanicus* occur outside our area of study (Europe). We consider *J. ranarius* and *J. ambiguus* to be synonymous.

Species name used by investigator	Origin of material	Chromosome number (2*n*)	Reference
J. bufonius L. agg.	Sweden	30	Hedberg & Hedberg (1964)
	Rumania	30	Tarnavschi (1948)
	Canada	34	Taylor & Mulligan (1968)
	Finland	c. 54	Hämet-Ahti & Virrankoski (1970)
	—	c. 60	Delay (1947a, 1947b)
	—	c. 60	Rohweder (1937)
	Iceland	c.120	Löve & Löve (1948, 1956)
J. bufonius L. sensu stricto	Finland	c. 54	Ahti & Hämet-Ahti (1971)
	Germany	c. 60	Wulff (1937)
	Denmark	80	Jörgensen *et al.* (1958)
	—	80	Segal (1962)
	Czechoslovakia	80	Uhrikova (1974)
	Netherlands	100–110	Loenhoud & Sterk (1976)
	—	100–110	Snogerup (1971)
	—	104–106	Snogerup (1959)
	Sweden	106	Weimarck (1963)
	Canada	106	Löve & Löve (1981)
	Canada	106	Löve *et al.* (1980)
	U.S.A.	c. 108	Harriman & Redmond (1976)
J. minutulus Alb. & Jah.	Netherlands	c. 70	Loenhoud & Sterk (1976)
	?Iran	72	Snogerup (1971)
J. minutulus Krecz. & Gonch.	—	30	Podlech & Dieterle (1969)
J. nastanthus Krecz. & Gonch.	—	60	Podlech & Dieterle (1969)
J. ranarius Song. & Perr.	Denmark	30	Jörgensen *et al.* (1958)
	Greenland	30	Jörgensen *et al.* (1958)
	—	34	Snogerup (pers. comm. 1967,
	Sweden	34	Weimarck (1963)
	Canada	34	Löve & Löve (1981)
	Netherlands	34	Loenhoud & Sterk (1976)
	Germany	c. 108–120	Wulff (1937)
J. ambiguus Guss.	—	30	Segal (1962)
	—	32	Segal (1962)
	Colorado, U.S.A.	34	Löve *et al.* (1971)
	Iceland	34	Löve (1970)
J. hybridus Brot.	?Iran	34	Snogerup (1971)
J. rechingeri Snog.	Afghanistan	30	Snogerup (1971)
J. turkistanicus Krecz. & Gonch.	Afghanistan	30	Podlech & Dieterle (1969)

The object of this paper is to outline the results of chromosome studies – both meiotic and somatic – and breeding experiments, and briefly to discuss the bearing these have on the evolution of the group.

Numerous chromosome counts have been provided by earlier workers (Table 1) but, since many of them are imprecise and derived from material whose correct identity has not been verified, they were discounted when chromosome numbers were given in the first of this series of papers (Cope & Stace 1978).

TABLE 2. CHROMOSOME NUMBERS OF THE *JUNCUS BUFONIUS* AGGREGATE DETERMINED DURING THIS STUDY

Somatic counts given as 2n, meiotic counts as n. Vouchers are in **MANCH** in addition to those indicated in the Table.

Juncus bufonius L. sensu stricto	
J371 – Knockbrandon, Co. Wexford, v.c. H12, Eire	n=54
SL1 – Merebere, Holbeck, Belgium	n=54
SL4 – Chilly-sur-Salins, Jura, France	n=54
SL10 – Pohjois – Pohjanmaa, Österbotten, Finland	n=54
SL13 – Ficuzza, Palermo, Sicily	n=54
Juncus foliosus Desf.	
J199 – Port, N. of Glencolmalle, W. Donegal, v.c. H35, Eire	2n=26
J313 – Rathlough, E. Donegal, v.c. H34, Eire	2n=26
J355 – Ardmore to Kilkearan,.W. Galway, v.c. H16, Eire	2n=26
J370 – Bargy Commons, Co. Wexford, v.c. H12, Eire	2n=26
J372 – Ballyknockan, Co. Wicklow, v.c. H20, Eire	2n=26
J373 – Near Laragh, Co. Wicklow, v.c. H20, Eire	2n=26
J393 – Barmouth, Merioneth, v.c. 48, Wales	2n=26
J584 – Llyn Peris, Caernarvonshire, v.c. 49, Wales	2n=26
Juncus ambiguus Guss.	
J334 – Lady's Island Lake, Co. Wexford, v.c. H12, Eire	2n=34
J359 – Smerwick Harbour, S. Kerry, v.c. H1, Eire	2n=34
J360 – Ballymacoda, E. Cork, v.c. H5, Eire	2n=34
Juncus hybridus Brot.	
J212 – San Nicola, Messina to Villafranca, Messina, Sicily (**LTR**)	n=17
J214 – San Nicola, Messina to Villafranca, Messina, Sicily (**LTR**)	n=17
J391 – Near C'an Picafort, Mallorca, Spain (**LTR**)	2n=34
J392 – La Puebla del Rio to Isla Mayor, Sevilla, Spain (**LTR**)	2n=34
J599 – Terceira, Azores	2n=34
SL11 – Alfonte, Palermo, Sicily	n=17
Juncus sorrentinii Parl.	
J581 – Near Caniçal, Madeira	2n=8

MATERIALS AND METHODS

MATERIALS

We used a total of 85 accessions representing all five segregates of *J. bufonius* agg. that we recognize. These were collected as seed or sometimes living plants by us and correspondents, or acquired via international seed exchange schemes. Chromosome counts were achieved from 23 accessions, and full details of these are given in Table 2.

SOMATIC CHROMOSOMES

Somatic chromosomes proved to be the more problematical and some considerable experimentation was needed before satisfactory results were obtained. The initial problem encountered was that of preferential absorption of stain by cytoplasmic granules and oil droplets over the chromosomes themselves. The material did not respond well to conventional fixing, mordanting and staining procedures, so a new technique, derived from suggestions made by Thomas (1940) for use with difficult material in Rosaceae, was developed.

The three stages of fixing, mordanting and staining were achieved with a single solution modified from Carnoy's Solution (3 parts absolute alcohol: 1 part glacial acetic acid). The acetic acid fraction of Carnoy's Solution was replaced by a mixture comprising 9 parts saturated aceto-carmine in glacial acetic acid, and 1 part saturated ferric acetate in glacial acetic acid. Once root-tips had been treated they could be stored in this solution in a deep-freeze for up to 2 months without noticeable deterioration.

After fixation, a corresponding lack of response to conventional hydrolyzing agents was also experienced. Root-tips were therefore not hydrolyzed, reliance being placed instead on efficient tapping-out and smearing.

The full schedule is as follows:

1 Sow seeds on filter-paper in petri-dishes.
2 Water with tap-water and place in an incubator set at 20°C with a 24 hour photoperiod.
3 When roots are about 1 cm long place the petri-dishes in a 5°C refrigerator overnight to reduce activity in the meristem.
4 Restore seedlings to room-temperature for 2 hours to allow synchronized cell division to begin.
5 Collect root-tips at intervals of 20–30 mins during the 2 hours to determine the optimum recovery period after cold shock.
6 Fix root-tips in alcoholic iron-aceto-carmine for 48 hours at room-temperature. If need be, after fixation, root-tips can be transferred to fresh solution and stored in a deep-freeze until required.
7 Tap-out root-tips, smear and squash in fresh iron-aceto-carmine (omit the alcoholic fraction from the fixative).
8 Seal cover-glass with rubber solution.

Once preparation of the slide was complete it was scanned for chromosomes and suitable cells were immediately drawn and, if good enough, photographed. No satisfactory technique for preparing permanent slides was found.

MEIOTIC CHROMOSOMES

The only serious problem encountered with meiotic chromosomes, apart from those already described for somatic chromosomes, was discovering the time of day at which meiosis takes place. It was eventually established at about midday, but depended to a great extent on prevailing weather conditions. For meiotic counts, stages 6–8 of the schedule devised for somatic chromosomes were followed.

BREEDING EXPERIMENTS

In order to test relationships between the segregates, a considerable number of artificial cross-pollinations was performed, but the rate of success was very low. Full details of the experimental procedures are given here but discussion of the background relating to floral biology is reserved for later.

Our own observations indicated that *J. bufonius* agg. is almost exclusively cleistogamous, although on occasion the flowers open for 2–3 hours after anthesis. Meiosis commences 40–45 hours before anther dehiscence. Pollen maturation occurs during the day following meiosis. The larger anthers available during the period of pollen maturation were found to be too fragile for safe manipulation, so emasculation was performed on the day of meiosis. The flowers at this time are 3–4 mm long and tightly closed, with the overlapping tepal margins somewhat adherent. Care is needed when handling the flower because it readily disarticulates at the base of the pedicel.

Once the flower had been opened, the anthers were knocked off their filaments and brushed away. Pollen was collected from a mature flower which was inverted over a watchglass and tapped or shaken. The recipient flower was then inverted and gently dipped into the pollen. Sweeping up of pollen had to be avoided because the connection between ovary and stigma is extremely fragile. After pollination the flower was re-closed as far as possible and sealed in clear adhesive tape. Sealing is vital as it prevents both contamination by air-blown pollen and desiccation of the stigmas. Pollination was performed nearly two days before it would normally have taken place in the flower concerned, so pollen had to remain on the stigma during the latter's maturation. The success of cross-pollination therefore depended to some extent on the longevity of the pollen, a factor which remains unknown.

Nearly all interspecific combinations of male and female parent were attempted and the same strain of each species was used throughout. Because of practical difficulties, no cross-pollinations employing *J. sorrentinii* as female parent were possible.

TABLE 3. STOMATAL DIMENSIONS AND PLOIDY LEVEL IN THE *J. BUFONIUS* AGGREGATE

	Range of means of stomatal length (μm)	Overall mean stomatal length (μm)	Number of specimens	Ploidy level
J. bufonius sensu stricto	24–48	38±1	264	6x
J. foliosus	30–47	38±1	64	2x
J. ambiguus	23–39	30±<1	135	2x
J. hybridus	23–40	32±1	80	2x
J. sorrentinii	29–42	35	12	2x

RESULTS

CHROMOSOME COUNTS

The difficulties encountered in obtaining accurate chromosome counts are to some extent a reflection of chromosome morphology. No chromosome structure was visible through an ordinary light microscope and the chromosomes appear as poorly resolved circular bodies averaging 0·5–0·8 μm in diameter. They are thus visible only near the limit of resolution of the microscope and there is no reason to suppose that they are in fact spherical.

Chromosome counts (Table 2) were obtained from all five species, although they were obtained from both root-tips and pollen mother cells only in *J. hybridus*.

Counts reported in the literature were often quite different from those achieved during the present work, and the variation in number indicated hitherto did not become apparent. Published chromosome numbers for *J. ambiguus* are 2n=30, 32, 34 and c.108–120, but all counts made during the present study were 2n=34. Similarly, our counts for *J. bufonius* sensu stricto were all 2n=108 compared with 2n=30, 34, c.54, c.60, 80, 100–110 and c.120 reported in the literature. Only one count (2n=34) has been reported for *J. hybridus* and this we confirmed. Neither *J. foliosus* (2n=26) nor *J. sorrentinii* (2n=28) has previously been studied cytologically to our knowledge.

Karpechenko (1928) and Sax & Sax (1937) first reported the correlations between cell size and level of polyploidy, and suggested that stomatal dimension would prove to be a useful index of polyploidy. This approach was taken up in *Juncus* by Snogerup (1971), who investigated this relationship in the *J. bufonius* aggregate. He attempted to use the information to predict the chromosome number of *J. turkestanicus* and his prediction was, in fact, confirmed by a later chromosome count. Our own investigation, however, indicates a different correlation from that apparently demonstrated by Snogerup. Table 3 shows that mean values for stomatal length fall into three groups: *J. bufonius* sensu stricto and *J. foliosus* with relatively long stomata (overall means both 38 μm); *J. ambiguus* and *J. hybridus* with relatively short stomata (overall means 30 and 32 μm respectively); and finally *J. sorrentinii*, whose values (29–42 μm, overall mean 35 μm) are intermediate. The interesting point is that *J. foliosus*, with a low chromosome number, is more similar to *J. bufonius* sensu stricto, a high polyploid, than to either of the other taxa with low chromosome numbers. It may be worth pointing out that the two species with the longest stomata are both mesophytes, whereas those with short stomata are xerophytes (one, *J. hybridus*, a plant of dry places, the other *J. ambiguus*, a saltmarsh plant subject to physiological drought). Cope & Stace (1983) have given observations on the plasticity of stomatal length.

FLOWERING BEHAVIOUR

The inflorescence of *J. bufonius* agg. is basically cymose with upwards sequential development of flowers. The number of flowers produced by each monochasium is theoretically unlimited, although in *J. bufonius* agg. it rarely exceeds five or six. Exceptionally there may be as many as twelve; quite often there is only one.

The flower terminating the main axis emerges from the sheath of its subtending bract three days before anthesis and, on emergence, the next flowers, the lowest on each monochasium, are already visible. Meiosis occurs in the first flower on the day following emergence, usually at or about midday.

Meiosis seems to be more or less synchronous within a single anther with all pollen mother cells at the same stage (although Shah (1963) disagrees on this point). Meiosis between anthers of a single flower is not synchronous, however, and, in preparations of all six anthers made simultaneously at just the right time, all stages of meiosis can be seen.

After meiosis there is no appreciable pause before pollen mitosis begins, although between first and second meiotic divisions and between meiosis and mitosis the nuclei do enter a short interphase of about half an hour. There is no delay of up to 24 hours before pollen mitosis begins, as seen in some species of *Juncus* subgenus *Genuini* (J. W. Grimes 1975, pers. comm.). By mid-afternoon all six anthers contain 8-nucleate pollen mother cells. The nuclei are arranged four towards the centre of the cell and four at the periphery; the former are the generative nuclei (Malheiros, Castro & Camara 1947), and the latter the vegetative (tube) nuclei. Once this stage has been reached cytokinesis begins and maturation of the pollen grain continues throughout the following day; the four products of pollen mother cell division remain united in a tetrad and are dispersed as such. Anthesis occurs at about 40–45 hours after the beginning of meiosis, sometime between sunrise and 8 or 9 a.m. Dehiscence of the anther is by means of a terminal pore in each theca.

The lowest flower on the lower monachasium undergoes anthesis 24 hours after the first flower, and on the day following that the lowest flower on the upper monochasium is pollinated. Thereafter there is an interval of 2 days between pollination events in each monochasium, and events alternate between flowers on the two monochasia arising from each biparous node.

HYBRIDIZATION EXPERIMENTS

A total of 490 cross-pollinations were undertaken (Table 4) and these yielded 26 probable hybrid seeds. In each successful case *J. ambiguus* had served as the female parent, the male parents being *J. bufonius* sensu stricto, *J. foliosus* and *J. hybridus*; one capsule was obtained from each of these crosses and contained eleven, eight and seven seeds respectively. Only two of these 26 seeds were successfully germinated and both were from the *J. ambiguus* × *J. foliosus* cross. In some respects the plants which ultimately developed from these seeds were intermediate between the parents, but in others they were quite different from either. Most significantly, if the origin of the hybrid plants had not been known, they could quite easily have been mistaken for *J. bufonius* sensu stricto, although they were highly sterile.

Table 5 summarises the characteristics of the hybrids (the two plants were identical) compared with those of their parents. The most important differences were in the inflorescence and comprised enlarged monochasia of five or six flowers instead of three or fewer, a much more profusely branched inflorescence, and a much longer flowering period (June 20–October 11, about two months more than either parent). Neither mature seeds nor mature capsules were produced by the hybrids, although pollen showed a 100% staining with aceto-carmine, a situation found in many other sterile *Juncus* hybrids. In size, the pollen was closer to that of *J. ambiguus* than to that of *J. foliosus*.

The capsules themselves stopped developing when about two-thirds the length of the inner tepals. The larger ones were dissected and found to contain numerous aborted ovules and often a few apparently well-developed seeds. Twenty-five such capsules contained an average of 5·9 of these seeds, but on removal from the capsules they collapsed within a few hours.

TABLE 4. NUMBER OF FLOWERS CROSSED IN HYBRIDIZATION ATTEMPTS BETWEEN THE SEGREGATES OF THE *JUNCUS BUFONIUS* AGGREGATE

One capsule of each combination marked* was obtained; all other crosses were unsuccessful.

	Male parent				
Female parent	*J. bufonius*	*J. foliosus*	*J. ambiguus*	*J. hybridus*	*J. sorrentinii*
J. bufonius	—	45	43	53	1
J. foliosus	42	—	31	50	3
J. ambiguus	28*	35*	—	37*	2
J. hybridus	39	47	28	—	6
J. sorrentinii	0	0	0	0	—

TABLE 5. COMPARATIVE MORPHOLOGICAL CHARACTERS OF THE SEGREGATES *J. AMBIGUUS* AND *J. FOLIOSUS* AND THE HYBRID BETWEEN THEM

Measurements of the two species refer solely to plants of the parental strains grown alongside the hybrid plant.

	J. ambiguus	Hybrid	*J. foliosus*
Inflorescence	Sub-fasciculate	Remote-flowered	Remote-flowered
Mean number of flowers per monochasium	2·5	6·0	2·8
Apex of outer tepal	Acute	Acute	Acute
Apex of inner tepal	Rounded-mucronate	Subacute-mucronate	Subacute
Apex of capsule	Truncate	—	Truncate
Mean inner tepal: capsule ratio	0·93	—	1·02
Stripes on tepals	Absent	Weak or absent	Strong
Mean filament: anther ratio	1·17	1·00	0·35
Mean pollen diameter (μm)	40·98	41·23	48·05
Pollen stainability	100%	100%	100%
Seed morphology	Smooth, barrel-shaped	—	Ridged, obovoid
Mean seed size (μm)	390×310	—	500×330
Mean seed length:breadth ratio	1·26	—	1·53
Leaf width (mm)	0·5–1·0	1–1·5	2·0–3·0
Height of plant (cm)	18	22	15

Another interesting characteristic of the hybrid was the filament: anther ratio. Its mean was 1·00, but in fact it varied from 0·63 to 3·00, embracing not only much of the ranges of both *J. ambiguus* and *J. foliosus*, but also a large part of that of *J. bufonius* sensu stricto.

Cytologically, the hybrids were difficult in that they did not respond as well to the alcoholic iron-aceto-carmine stain-fixative developed for use with their parents. A prefixation of 24 hr in acetic-alcohol before stain-fixation went some way to ameliorating the problem.

The earliest meiotic phase seen was anaphase I, in which the expected total of 30 chromosomes was visible (from 2n=34 and 2n=26 in the parents). On many occasions three lagging chromosomes were seen, but sometimes there were fewer or none at all. At metaphase II, what appeared to be a multivalent structure comprising four chromosomes was seen in each nucleus. The apparent contradiction implied by these last two features is considered in the Discussion.

DISCUSSION

With chromosome numbers ranging from 2n=26 to 2n=108 or 120 in the *J. bufonius* aggregate, it is difficult to decide what the basic chromosome number for the aggregate, or even the genus, may be. An assessment of all known chromosome numbers in the genus *Juncus* reveals peaks of occurrence at n=15, 20, 30, 40 and 60 (31% of all numbers are 2n=40), i.e. multiples of 5, 10 or 15. As *J. decipiens* (Buch.) Nakai has 2n=20 and *J. capitatus* Weig. has 2n=18, it is probable that the basic number for *Juncus* is 5, a conclusion tentatively reached by Löve & Löve (1961). 63% of all numbers fall within the range n=13 to n=25, so clearly there is considerable aneuploidy in *Juncus*.

If the base number of the genus really is to be regarded as x=5, then no strictly diploid species (2n=10) are known to exist. Alternatively, one may consider *J. decipiens* (2n=20) and *J. capitatus* (2n=18) to be diploid or near-diploid. However, in view of the wide and frequent occurrence of aneuploidy, it seems best to consider each taxonomic group within *Juncus* separately, especially as the main features of chromosomal evolution differ between many of the subgenera. On this basis we have treated the species of the *J. bufonius* aggregate with chromosome numbers of 2n=26 and 2n=34 as near-diploids, *J. minutulus* and others in the range 2n=54–80 as tetraploids, and *J. bufonius* sensu stricto (2n=100–120) as hexaploids.

The *J. bufonius* aggregate therefore comprises taxa with at least three ploidy levels, with considerable aneuploidy exhibited at each. Since there is no single base number evident in the aggregate, interpretation of the higher numbers must remain conjectural, e.g. $2n=108$ could be a hexaploid based on $x=18$, but perhaps equally $2n=104$ could be an octoploid based on $x=13$. The precise degree of aneuploidy is similarly impossible to ascertain, because the extremely small size of the chromosomes prevents accurate counting at the higher levels other than in exceptionally favourable preparations.

Consideration of the possibly unusual course of meiosis in *Juncus* is likely to be relevant to an understanding of the evolution of the *J. bufonius* aggregate. Observations of meiotic behaviour in *Juncaceae* and *Cyperaceae* have revealed a level of similarity that has led certain authors to draw conclusions on the nature of the meiosis and structure of the chromosome in *Juncus* from behaviour seen in *Carex*, *Scirpus* and *Luzula*.

The earliest references relating to this aspect come from Heilborn (1928) and Wahl (1940), who worked on *Carex*, and Nordenskiöld (1951), who studied *Luzula*. Having noted the absence of lagging chromosomes at anaphase I in certain hybrids, these authors concluded that meiosis in the taxa concerned was 'inverted', i.e. the equational division preceded the reductional. Battaglia & Boyes (1955) doubted that this was the case in *Carex* but considered it to be so in *Juncus*. Wahl (1940) suggested that inverted meiosis occurred in all Cyperaceae, even though Tanaka (1937, 1938, 1939a,b,c, 1940a,b, 1949) stated that bivalents segregated at anaphase I in *Scirpus*. Malheiros *et al.* (1947) thought inverted meiosis was common to all members of both Cyperaceae and Juncaceae. Davies (1956) and Faulkner (1972) have confirmed that it does indeed occur in *Carex*.

Battaglia & Boyes (1955) have fully described inverted meiosis in *Luzula* (although they referred to it as "post-reductional meiosis"). The important point is that at metaphase I each chromosome is auto-orientated with its two chromatids directed to opposite poles, so that first division is, as a result, equational. If the first division is indeed equational and chiasmata are formed from chromatids originating from different chromosomes (Swanson 1958), then it follows that multivalent configurations should be visible at both metaphase I and metaphase II (Nordenskiöld 1962).

The possession of aneuploid series of chromosome numbers in Cyperaceae and Juncaceae is normally attributed to the presence of a non-localized centromere. Apart from the dicentric chromosomes reported by Piza (1939, 1941) and Malheiros & Castro (1947) in *Luzula purpurea* (Marson ex Buch.) Link (=*L. elegans* Lowe), there are two further possible conditions summarized by Rhoades & Kerr (1949). The 'diffuse centromere' (Löve *et al.* 1957) was described as having sites for spindle-fibre attachment spread throughout the length of the body of the chromosome, while the 'polycentric chromosome' (Godward 1951; LaCour 1953) was envisaged as end-to-end union of extremely small metacentric chromosomes. Malheiros *et al.* (1947) considered the evidence in favour of either type in most examples to be inadequate and preferred to call them both 'non-localized centromeres'.

Heilborn (1924) showed that the chromosomes of *Carex* were without centromeric constrictions, a feature later confirmed by Davies (1956). The absence of a centromere in *Luzula* was demonstrated by Malheiros & Castro (1947), Malheiros *et al.* (1947), Castro (1950) and Castro & Noronho-Wagner (1952), and experimentally confirmed by Castro *et al.* (1948, 1949a, 1949b) and Nordenskiöld (1962). After exposing chromosomes to X-rays, these authors observed that the fragments so produced retained mobility at anaphase. A similar experiment, with the same result, was conducted on *Eleocharis palustris* (L.) Roem. & Schult. by Håkansson (1954, 1958). Further reports of a non-localized centromere in *Luzula* come from Östergren (1949), Berger (1949), Brown (1950) and Thomas (1950).

That there is a non-localized centromere in *Juncus* is now generally accepted (Löve & Löve 1944; Malheiros-Gardé & Gardé 1951; but see also Grant (1971, p. 269) for a conflicting view), but it has never been confirmed experimentally. One reason for supposing it might be present is the existence of aneuploids which all seem to behave as conventional diploids. Löve *et al.* (1957) noted that in *Carex* the frequency of large chromosomes decreased with an increase in chromosome number. A similar correlation was found in *Luzula* by Malheiros & Gardé (1947), Nordenskiöld (1949, 1951), Wagner (1949) and Halkka (1964). This correlation has been attributed to fragmentation of single chromosomes or whole chromosome sets, and the survival of the fragments, which is only possible in chromosomes with a non-localized centromere. The phenomenon was called 'agmatoploidy' by Malheiros-Gardé & Gardé (1950) and Nordenskiöld (1956), 'endonuclear polyploidy' by Nordenskiöld (1951), and 'pseudopolyploidy' by Battaglia (1956). Agmatoploidy thus signifies an increase in chromosome number without any attendant increase in total chromatin mass or chromatid length (Nordenskiöld 1951; Löve *et al.* 1957; Halkka 1964). We consider that our measurements are not sufficiently accurate to ascertain whether this inverse correlation between chromosome size and number holds true for *J. bufonius* agg. DNA estimation would be desirable.

Certain aneuploids in *Luzula* (Nordenskiöld 1951; Löve *et al.* 1957), *Carex* (Heilborn 1924) and *Scirpus* (Tanaka 1938) are thought to be derived by chromosome fragmentation and are therefore incomplete endonuclear polyploids (agmatoploids); they are quite different from the aneuploids originally circumscribed by Winge (1917, 1940), in which increases or decreases in DNA content are involved.

A number of authors, among them Malheiros *et al.* (1947), Castro *et al.* (1949a, 1949b), Malheiros-Gardé & Gardé (1951), Nordenskiöld (1951) and Davies (1956), have indicated an apparent correlation between the occurrence of a non-localized centromere and inverted meiosis. Castro (1950) went so far as to claim that such a centromere was essential for inverted meiosis. In the Odonata, however, where inverted meiosis is known to occur, the chromosomes each have a single localized centromere (Oksala 1943, 1944).

The evidence for either a non-localized centromere or inverted meiosis in the *J. bufonius* aggregate is still very inconclusive. That no centromere was seen in any chromosome is no evidence that one does not exist, since observation was subject to two severely limiting factors: the method of preparation and the level of microscopic resolution. Our evidence on this point was not only equivocal but sometimes contradictory. The presence of an apparent multivalent at metaphase II in the synthesized hybrid suggests an inverted meiosis, but lagging chromosomes at anaphase I are exactly what one would expect from normal meiosis in a hybrid. Our work originally did not seek to investigate the existence in *J. bufonius* agg. of diffuse centromeres or inverted meiosis, but progress along these lines is now being pursued by one of us (C.A.S.) in *Juncus* subgenus *Genuini*.

On the basis of morphological and geographical data discussed in our earlier papers, and cytological data presented in this, we have established three lines of evidence for the nature of the *J. bufonius* aggregate. Firstly, *J. bufonius* sensu stricto is morphologically the most variable segregate and shows elements of all other European species in its structure. Secondly, *J. bufonius* sensu stricto is a polyploid with the behaviour of an allopolyploid, and presumably of hybrid origin; the other four segregates are considered to be diploid. Thirdly, *J. bufonius* sensu stricto is geographically and ecologically more diverse than any other single taxon, being wholly sympatric with all of them and occurring in places where they do not. These three features together indicate that the group as a whole represents a polyploid 'pillar' complex (Babcock & Stebbins 1938). Although we were not able to confirm an intermediate level of polyploidy between diploids and hexaploids, reports of numbers corresponding to a tetraploid level do appear in the literature, rather more than might be attributed to error alone. Thus it is reasonable to accept that taxa such as *J. minutulus* (which we do not separate taxonomically from *J. bufonius* sensu stricto) do represent the intermediate, tetraploid level. *J. bufonius* sensu stricto is envisaged as having arisen from a sequence of hybridization events, in association with amphidiploidization, from diploid taxa which interbred to form tetraploids. These in turn back-crossed to the diploids to form hexaploids and possibly interbred amongst themselves to form octoploids.

Therefore we believe that *J. bufonius* sensu stricto (including *J. minutulus*) arose from a pool of diploids, including the four included in our studies. It is likely that this origin was both polytopic and a long-continuing process. The ranges of the European diploids overlap at present across a wide area of the western Mediterranean, and there is no reason to believe that *J. bufonius* sensu stricto originated from only a part of this area. However, the Middle Eastern diploid, *J. rechingeri*, which is part of the aggregate, has certain distinctive features, such as a characteristic tepal morphology and testa sculpturing, and a lack of cauline leaves, not found in *J. bufonius* sensu stricto, which suggests that *J. rechingeri* (and perhaps other taxa in that area) has not contributed to the gene-pool of *J. bufonius* sensu stricto. On the other hand, it is probable that the original diploid gene-pool was quite different (possibly more diverse) from that found in the western Mediterranean today.

Some direct evidence for the origin of *J. bufonius* sensu stricto has come from our hybridization experiments. The single synthetic hybrid we produced was completely sterile. Nevertheless, it was morphologically so like *J. bufonius* sensu stricto that it is easy to speculate that, had it been a fertile amphidiploid, it would have been quite indistinguishable from it. Probably many plants ascribed to *J. bufonius* sensu stricto are fertile allotetraploids of this sort; one such plant is possibly *J. minutulus*. If this is so, then new variants of *J. bufonius* sensu stricto are probably still arising today.

REFERENCES

Ahti, T. & Hämet-Ahti, L. (1971). Hemerophilous flora of the Kuusamo District, N. E. Finland and the adjacent part of Karelia, and its origin. *Ann. Bot. Fennici*, **8**: 34.

Babcock, E. B. & Stebbins, G. L. (1938). The American species of *Crepis*: their relationships and distribution as affected by polyploidy and apomixis. *Carnegie Inst. Washington Publ.*, **504**.

Battaglia, E. (1956). The concept of pseudopolyploidy. *Caryologia*, **8**: 214–220.

Battaglia, E. & Boyes, J. W. (1955). Post-reductional meiosis: its mechanism and causes. *Caryologia*, **8**: 87–134.

Berger, C. A. (1949). The cytology of *Luzula*. *Am. J. Bot.*, **36**: 794.

Brown, C. W. (1950). Spurious secondary association and asymmetric spindles in a *Luzula*. *Cytologia*, **15**: 259–268.

Castro, D. de (1950). Notes on two cytological problems of the genus *Luzula* DC. *Genet. iber.*, **2**: 201–209.

Castro, D. de, Câmara, A. & Malheiros, N. (1948). X-rays in the centromere problem of *Luzula purpurea* Link. *Int. Conf. Genet.*, **8**: 548–550.

Castro, D. de, Câmara, A. & Malheiros, N. (1949a). X-rays in the centromere problem of *Luzula purpurea* Link. *Genet. iber.*, **1**: 49–54.

Castro, D. de, Câmara, A. & Malheiros, N. (1949b). X-rays in the centromere problem of *Luzula purpurea* Link. *Hereditas*, suppl. vol. **35**: 548–550.

Castro, D. & Noronho-Wagner, N. (1952). Nota sobre a perpetuaçao de fragmentos cromosomicos e *Luzula purpurea*. *Agronomia lusit.*, **14**: 95–99.

Cope, T. A. & Stace, C. A. (1978). The *Juncus bufonius* L. aggregate in western Europe. *Watsonia*, **12**: 113–128.

Cope, T. A. & Stace, C. A. (1983). Variation in the *Juncus bufonius* L. aggregate in western Europe. *Watsonia*, **14**: 263–272.

Davies, E. W. (1956). Cytology, evolution and origin of the aneuploid series in the genus *Carex*. *Hereditas*, **42**: 349–365.

Delay, C. (1947a). Recherches sur la structure des noyaux quiescents chez les phanérogames. *Revue Cytol. Cytophysiol. vég.*, **9**: 169–223.

Delay, C. (1947b). Recherches sur la structure des noyaux quiescents chez les phanérogames. *Revue Cytol. Cytophysiol. vég.*, **10**: 103–229.

Faulkner, J. S. (1972). Chromosome studies on *Carex* section *Acutae* in northwest Europe. *Bot. J. Linn. Soc.*, **65**: 271–301.

Godward, M. B. E. (1951). Compound chromosomes and polyploidy in *Spirogyra*. *Heredity, Lond.*, **5**: 158–159.

Grant, V. (1971). *Plant speciation*. New York & London.

Håkansson, A. (1954). Meiosis and pollen mitosis in X-rayed and untreated spikelets of *Eleocharis palustris*. *Hereditas*, **40**: 325–345.

Håkansson, A. (1958). Holocentric chromosomes in *Eleocharis*. *Hereditas*, **44**: 531–540.

Halkka, O. (1964). A photometric study of the *Luzula* problem. *Hereditas*, **52**: 81–88.

Hämet-Ahti, L. & Virrankoski, V. (1970). Chromosome numbers of some vascular plants of North Finland. *Ann. Bot. Fennici*, **7**: 177–181.

Harriman, N. A. & Redmond, D. (1976). Somatic chromosome numbers for some North American species of *Juncus*. *Rhodora*, **78**: 727–738.

Hedberg, I. & Hedberg, O. (1964). Documented chromosome numbers of Swedish plants. *Svensk bot. Tidskr.*, **58**: 125.

Heilborn, O. (1924). Chromosome numbers and dimensions, species formation and phylogeny in the genus *Carex*. *Hereditas*, **5**: 129–216.

Heilborn, O. (1928). Chromosome studies in Cyperaceae. *Hereditas*, **11**: 182–192.

Jörgensen, C. A., Sörensen, T. & Westergaard, M. (1958). The flowering plants of Greenland, a taxonomical and cytological survey. *Biol. Skr.*, **9(4)**: 1–172.

KARPECHENKO, G. D. (1928). Polyploid hybrids of *Raphanus sativus* × *Brassica oleracea* L. *Z.indukt. Abstamm.- u. VererbLehre*, **48**: 1–85.

LACOUR, L. F. (1953). The *Luzula* system analysed by X-rays. *Heredity*, suppl. vol. **6**: 77–81.

LAURENT, M. (1904). Recherches sur le développement des Joncées. *Annls Sci. Nat., Bot.*, Sér. 8, **19**: 97–194.

LOENHOUD, P. J. VAN & STERK, A. A. (1976). A study of the *Juncus bufonius* complex in the Netherlands. *Acta bot. Neerl.*, **25**: 193–204.

LÖVE, Á. (1970). *Islenzk Ferdaflóra*, p. 178. Reykjavík.

LÖVE, Á. & LÖVE, D. (1944). Cytotaxonomic studies on Boreal plants, 2: Some notes on the chromosome numbers of Juncaceae. *Arkiv för botanik*, **31B(1)**: 1–6.

LÖVE, Á. & LÖVE, D. (1948). *Chromosome numbers of northern plant species*. Reykjavík.

LÖVE, Á. & LÖVE, D. (1956). Cytotaxonomical conspectus of the Icelandic flora. *Acta Horti Gothoburg.*, **20**: 65–291.

LÖVE, Á. & LÖVE, D. (1961). Chromosome numbers of Central and Northwest European plant species. *Op. bot. Soc. bot. Lund*, **5**: 92–96.

LÖVE, Á. & LÖVE, D. (1981). In LÖVE, Á. Chromosome number reports, LXXIII. *Taxon*, **30**: 829–861.

LÖVE, Á., LÖVE, D. & BERNARD, J.-P. (1980). In LÖVE, Á. Chromosome number reports, LXIX. *Taxon*, **29**: 703–730.

LÖVE, Á., LÖVE, D. & KAPOOR, B. M. (1971). Cytotaxonomy of a century of Rocky Mountain orophytes. *Arctic Alpine Res.*, **3**: 139–165.

LÖVE, Á., LÖVE, D. & RAYMOND, M. (1957). Cytotaxonomy of *Carex*, section *Capillares*. *Can. J. Bot.*, **35**: 715–761.

MALHEIROS, N. & CASTRO, D. DE (1947). Chromosome number and behaviour in *Luzula purpurea* Link. *Nature*, **160**: 156.

MALHEIROS, N., CASTRO, D. DE & CAMARA, A. (1947). Cromosomas san centrómero localizado. O casa da *Luzula purpurea* Link. *Agronomia lusit.*, **9**: 51–71.

MALHEIROS, N. & GARDÉ, A. (1947). Contribuiçôes para o estudo citológico do género *Luzula* Link. *Agronomia lusit.*, **9**: 75–79.

MALHEIROS-GARDÉ, N. & GARDÉ, A. (1950). Fragmentation as a possible evolutionary process in the genus *Luzula* DC. *Genet. iber.*, **2**: 257–262.

MALHEIROS-GARDÉ, N. & GARDÉ, A. (1951). Agmatoploidia no género *Luzula* DC. *Genet. iber.*, **3**: 155–176.

NORDENSKIÖLD, H. (1949). The somatic chromosomes of some *Luzula* species. *Bot. Notiser*, **102**: 81–92.

NORDENSKIÖLD, H. (1951). Cyto-taxonomical studies in the genus *Luzula*, I. Somatic chromosomes and chromosome numbers. *Hereditas*, **37**: 325–355.

NORDENSKIÖLD, H. (1956). Cyto-taxonomical studies in the genus *Luzula*, II. Hybridization experiments in the *campestris-multiflora* complex. *Hereditas*, **42**: 7–73.

NORDENSKIÖLD, H. (1962). Studies of meiosis in *Luzula purpurea*. *Hereditas*, **48**: 503–519.

OKSALA, T. (1943). Zytologische Studien an Odonaten, I. Chromosomenverhältnisse bei der Gattung *Aeschna* mit besonderer Berücksichtigung der postreduktionellen Teilung der Bivalente. *Suomal. Tiedeakat. Toim.*, A. IV, **4**: 1–64.

OKSALA, T. (1944). Zytologische Studien an Odonaten, II. Die Entstehung der meiotischen Präkozität. *Suomal. Tiedeakat. Toim.*, A. IV, **5**: 1–37.

ÖSTERGREN, G. (1949). *Luzula* and the mechanism of chromosome movements. *Hereditas*, **35** 445–468.

PIZA, S. DE T. (1939). Compotamento dos cromossômios na primeira divisão do espermatócito do *Tityus bahiensis*. *Scientia genet.*, **1**: 255–261.

PIZA, S. DE T. (1941). Chromosomes with two spindle attachments. *J. Hered.*, **32**: 423–426.

PODLECH, D. & DIETERLE, A. (1969). Chromosomenstudien an afghanischen Pflanzen. *Candollea*, **24**: 185–243.

RHOADES, M. M. & KERR, W. E. (1949). A note on centromere organisation. *Proc. natn. Acad. Sci. U.S.A.*, **35**: 129–132.

ROHWEDER, H. (1937). Versuch zur Erfassung der mengenmässigen Bedeckung des Darss und Zingst. *Planta*, **27**: 501–549.

SAX, K. & SAX, H. J. (1937). Stomata size and distribution in diploid and polyploid plants. *J. Arnold Arbor.*, **18**: 164–172.

SEGAL, S. (1962). Het soortsbegrip bij het *Juncus bufonius* complex. *Jaarb. K. ned. Bot. Vereen.*, **1962**: 58–59.

SHAH, C. K. (1963). The life history of *Juncus bufonius*. *J. Indian bot. Soc.*, **42**: 238–251.

SNOGERUP, S. (1959). In DAHLGREN, R. Från Lunds Botaniska Förenings Förhandlinger 1958. *Bot. Notiser*, **112**: 101–110.

SNOGERUP, S. (1971). *Juncus*, in RECHINGER, K. H., ed. *Flora Iranica*, **75**: 15–18. Graz.

SWANSON, C. P. (1958). *Cytology and cytogenetics*. London.

TANAKA, N. (1937). Chromosomes of *Scirpus lacustris* L. (prel. note). *Jap. J. Genet.*, **13**: 254.

TANAKA, N. (1938). Chromosome studies in Cyperaceae, III. *Scirpus lacustris* L. *Cytologia*, **8**: 515–520.

TANAKA, N. (1939a). Chromosome studies in Cyperaceae, IV. The maturation divisions in *Scirpus lacustris* L. with special reference to the heteromorphic pairing. *Cytologia*, **9**: 533–566.

Tanaka, N. (1939b). Cytological studies in the genus *Carex*. A collective review. *Jap. J. Genet.*, **15**: 96–104.

Tanaka, N. (1939c). Chromosome studies in Cyperaceae, V. Pollen development of *Carex grallatoria* Maxim. var. *heteroclita* Kükenth. ex Matsum. *Jap. J. Genet.*, **15**: 153–157.

Tanaka, N. (1940a). Chromosome studies in Cyperaceae, VI. Pollen development and additional evidence for the compound chromosome in *Scirpus lacustris* L. *Cytologia*, **10**: 348–362.

Tanaka, N. (1940b). Chromosome studies in Cyperaceae, VIII. Meiosis in diploid and tetraploid forms of *Carex siderosticta* Hance. *Cytologia*, **11**: 282–310.

Tanaka, N. (1949). Chromosome studies in the genus *Carex*, with special reference to aneuploidy and polyploidy. *Cytologia*, **15**: 15–29.

Tarnavschi, I. T. (1948). Die chromosomenzahlen der Anthophyten-Flora von Rümänien mit ausblick auf das polyploidie problem. *Bul. Grăd. bot. Muz. bot. Univ. Cluj*, **28**, suppl. **1**: 130.

Taylor, R. L. & Mulligan, G. A. (1968). *Flora of the Queen Charlotte Islands*, **2**, p. 43. Ottawa.

Thomas, P. T. (1940). The aceto-carmine method for fruit material. *Stain Technol.*, **15**: 167–172.

Thomas, P. T. (1950). Centromere precocity in *Luzula*. *Heredity*, **4**: 137–138.

Uhrikova, A. (1974). In Májovský, J. *et al.* Index of chromosome numbers of Slovakian flora (Part 4). *Acta Fac. Rerum Nat. Univ. Comenianae Bot.*, **23**: 1–23.

Wagner, M. de N. (1949). Subsídio para o estudo citológico do género *Luzula* D.C. *Genet. iber.*, **1**: 59–67.

Wahl, H. A. (1940). Chromosome numbers and meiosis in the genus *Carex*. *Am. J. Bot.*, **27**: 458–470.

Weimarck, H. (1963). *Skånes Flora*, p. 71. Lund.

Winge, Ö. (1917). The chromosomes. Their numbers and general importance. *C.r. Trav. Lab. Carlsberg*, **13**: 131–275.

Winge, Ö. (1940). Taxonomic and evolutionary studies in *Erophila* based on cytogenetic investigations. *C.r. Trav. Lab. Carlsberg*, **23**: 41–74.

Wulff, H. D. (1937). Karyologische Untersuchungen au der Halophyten-flora Schleswig-Holsteins. *Jb. wiss. Bot..*, **84**: 812–840.

(*Accepted August 1984*)

A reappraisal of the British and Irish dactylorchids, 2. The diploid marsh-orchids

R. M. BATEMAN

Geology Department, Royal Holloway College, Egham, Surrey, TW20 0FX

and

I. DENHOLM

Rothamsted Experimental Station, Harpenden, Herts., AL5 2JQ

ABSTRACT

52 morphological characters were recorded for 169 individuals from 17 British and Irish populations of diploid marsh-orchids. Multivariate analysis suggested that they should be referred to a single species, *Dactylorhiza incarnata* (L.) Soó. Five infraspecific taxa are best treated at subspecific rank: subsp. *incarnata* (L.) Soó, subsp. *coccinea* (Pugsley) Soó, subsp. *cruenta* (O. F. Müller) P. D. Sell, subsp. *pulchella* (Druce) Soó and subsp. *ochroleuca* (Wüstnei ex Boll) Heslop-Harrison f. A new combination, **D. incarnata** subsp. **incarnata** f. **punctata** (Vermeulen) Bateman & Denholm, **comb. nov.**, is proposed. These subspecies showed differing amounts of morphological overlap, which increased considerably when floral pigmentation characters were excluded from the analysis; only *D. incarnata* subsp. *ochroleuca* remained distinct. The other subspecies show only partial morphological differentiation and ecological specialization. A pigmentation scheme is presented to account for the remarkable variation in flower colour. Several supposedly diagnostic characters of *D. incarnata* or its subspecies were found to be unsatisfactory. Possible mechanisms responsible for maintaining the extensive morphological variation within *D. incarnata* are discussed. Principal coordinates provided the basis for revised diagnostic descriptions of *D. incarnata* and its British and Irish subspecies. These are compared with descriptions of Continental plants in an attempt to resolve several taxonomic and nomenclatural controversies. Suitable areas for further research are outlined.

INTRODUCTION AND TAXONOMIC HISTORY

British and Irish diploid marsh-orchids are now generally assigned to a single species, *Dactylorhiza incarnata* (L.) Soó (Early Marsh-orchid). The exceptional variation shown by the diploid marsh-orchids has resulted in the recognition of several morphologically and ecologically differentiated taxa. Table 1 compares 15 previous taxonomic treatments with our classification, and lists authorities for each taxon. *D. incarnata* subspp. *incarnata, coccinea, pulchella* and *ochroleuca* (or synonymous taxa) were treated at varietal rank by early workers (Camus & Camus 1929; Pugsley 1935) but were elevated to subspecies in most subsequent classifications. *D. incarnata* subsp. *gemmana* was given subspecific status only by Heslop-Harrison (1954, 1956), and was omitted from several classifications. *D. incarnata* subsp. *cruenta* was regarded as a full species by most orchidologists, but was relegated to a subspecies of *D. incarnata* by Heslop-Harrison (1954, 1956) and more recently by Sundermann (1980) and Soó (1980).

Most of these classifications were based on a qualitative examination of live or herbarium specimens and were therefore too subjective. Only Heslop-Harrison (1956) attempted to resolve the problem biometrically, but he measured relatively few characters and compared only population means. This method does not take proper account of the extensive variation present within dactylorchid populations;[1] apparently significant differences in population means for

---

[1] We regard both populations and colonies as spatially isolated aggregates of dactylorchids. However, whereas a population consists of freely-interbreeding individuals of a single species, a colony may comprise two or more coexisting populations (i.e. more than one species).

TABLE 1. COMPARISON OF OUR CLASSIFICATION WITH 14 OTHER TAXONOMIC TREATMENTS OF THE DIPLOID MARSH-ORCHIDS

	British authors				Continental authors						
TAXA (AND SYNONYMS)	Pugsley (1935)	Clapham (1952)	Summerhayes (1951) Hunt & Summerhayes (1965)	Heslop-Harrison (1954, 1956) Clapham (1962) Davies *et al.* (1983)	Camus & Camus (1929)	Soó (1962)	Senghas (1968)	Nelson (1976)	Landwehr (1977)	Sundermann (1980)	Soó (1980)
D. incarnata											
subsp. *incarnata* (L.) Soó (*lanceata, strictifolia*)	var.[2]	subsp.	subsp.	subsp.	var.[2]	subsp.	subsp.	subsp.	subsp.	subsp.	subsp.
'subsp. *gemmana* (Pugsley) Heslop-Harrison f.'[1] (*latissima, macrophylla*)	var.	—		subsp.	—	var.	var.	—	var.	—	—
subsp. *ochroleuca* (Wüstnei ex Boll) P. F. Hunt & Summerhayes (*straminea*)	var.	—	subsp.	subsp.	var.	var.	subsp.	subsp.	subsp.	var.	subsp.[3]
subsp. *coccinea* (Pugsley) Soó (*dunensis*)	var.	subsp.	subsp.	subsp.	var.	subsp.	subsp.	subsp.	subsp.	subsp.	subsp.
subsp. *pulchella* (Druce) Soó (*cambrica*)	var.	var.	subsp.	subsp.	var.	subsp.	subsp.	var.[3]	var.	var.	subsp.
subsp. *cruenta* (O. F. Müller) P. D. Sell	sp.	sp.	sp.	subsp.	sp.	sp.	sp.	sp.	sp.	subsp.	subsp.

[1] Status uncertain.
[2] Type variety not formally described.
[3] Discussed at this taxonomic rank but not formally described.

characters conceal important intra-population variation (Bateman & Denholm 1983a). To overcome this difficulty we measured many morphological characters in representative samples of several diploid marsh-orchid populations and used principal coordinates to analyze data for individual plants. The results provide an objective assessment of the phenetic similarities of individuals, and the amount of separation or overlap of groups of individuals on principal coordinates plots provides a quantitative basis for assessing their taxonomic status (Bateman & Denholm 1983a).

The classification suggested by the results of the present study (shown in the left-hand column of Table 1) is used throughout the paper.

MATERIALS AND METHODS

17 diploid marsh-orchid populations were sampled during 1981 and 1982, including populations of five of the six taxa listed in Table 1 (*D. incarnata* subsp. *gemmana* was not examined). Details of these populations and the sample localities are presented in Table 2.

Morphological characters were recorded for each of ten flowering plants per population, which were chosen randomly in the 11 colonies that contained only one colour variant of *D. incarnata* (Table 2). At five of the six remaining localities, random sampling was performed only within areas where a particular colour variant formed pure stands, and at Wicken nine yellow-flowered plants growing alongside abundant pink- and purple-flowered *D. incarnata* were deliberately selected. Vegetative characters were scored in the field. Floral and bract cell data were obtained within two days of sampling from a single flower, preferably excised when fully open from halfway up the inflorescence. Destructive studies of tuberoids and stem cavities were not attempted. The 52 quantitative and qualitative (scaled) characters that were recorded largely follow Bateman & Denholm (1983a). However, character 30a (ovary length) replaces character 30 (inflorescence width) and there is an additional character (=39a, position of longest leaf along stem). Fig. 1 illustrates many of the following characters:

A. *Labellum* (14 characters).

All except character 7 were taken from flattened mounted labella. Labellum colour was measured immediately after mounting as it subsequently deepened rapidly. The base colour of the lower part of each labellum was matched to the nearest colour block of the Royal Horticultural Society Colour Chart (Anon. 1966) and converted to three C.I.E. (Commission Internationale de l'Eclairage) coordinates. Two of these ('x' and 'y') define a position on a square grid superimposed on to a triangular array of colours which pale towards white at the centre of the triangle. The corners correspond to pure blue, pure green and pure red (Fig. 2). Density of pigment is measured by a third coordinate (reflectivity, 'Y'), which decreases in value from the centre of the triangle outwards and is represented on Fig. 2 by dashed contours.

1. Length, from spur entrance to apex of central lobe.
2. Presence (1) or absence (0) of sinuses separating central and lateral lobes (i.e. three-lobed or entire labella).
3. Length, from base of spur entrance to base of sinus (if present).
4. Length, from base of spur entrance to apex of right lateral lobe (if sinuses present).
5. Maximum width.
6. Position of maximum width in relation to axis of maximum length, on a scale 1–3 (1=above middle; 2=±at middle; 3=below middle).
7. Amount of reflexion of lateral lobes, on a scale 1–6 (1=slightly deflexed through to 6=completely reflexed).
8. Colour, x (arbitrary values ranging from 100 to 600).
9. Colour, y (arbitrary values ranging from 100 to 600).
10. Colour, percentage reflectivity (Y).
11. Type of markings, on a scale 0–5 (0=no markings; 1=spots; 2=spots and dashes; 3=dashes and loops; 4=loops; 5=±solid blotch).
12. Distribution of markings, on a scale 0–3 (0=no markings through to 3=extensive coverage).

TABLE 2. DETAILS OF SAMPLE LOCALITIES AND STUDY POPULATIONS

Subspecies	Habitat and locality	Grid reference	Altitude (m O.D.)	Soil parent materials	Soil pH (in H_2O)	Approx. no. of plants	Peak flowering period^1	Presence (and frequency) of other dactylorchids^2
incarnata	Meadow, BLAGROVE Common, Sandon, Herts., v.c. 20	52/326.337	135	Till	6·3–7·5	4000	5/4–6/1	FF(c) FF×MPr(o) MPr(f) MPr×II(vr) FF×II(r)
	Marsh, Rushy Meadow, TRING Rural, Herts., v.c. 20	42/907.127	105	Peat & alluvium/ chalk	7·6	16	6/1	MPr(o) FF×MPr(vr)
	Marsh, W. LLYN RHOS-DDU, Newborough, Anglesey, v.c. 52	23/420.645	10	Peat/Precambrian schist & gneiss	—	15	5/4–6/1	MP(o)
coccinea	Marshy meadow, RHOS-Y-GAD, Pentraeth, Anglesey, v.c. 52	23/510.788	35	Peat/till	6·8	50	6/1	IP(vr) MP(o) FF(o) MT(f) McE(o) McE×MP(vr) FF×MP(vr)
	Dune slack, NEWBOROUGH Warren, Anglesey, v.c. 52	23/424.621	10	Blown sand/Precambrian schist & gneiss	7·6	5000	5/4	MP(o) FF×MP(vr)
	Marshy meadow by Cob Pool, MALLTRAETH, Anglesey, v.c. 52	23/410.680	1	Peat and blown sand/ coal measures	7·2	70	6/1	MP(f) FF×MP(vr)
	Dune slack, AINSDALE, S. Lancs., v.c. 59	34/296.120	3	Blown sand/Keuper marl	8·1	1000	6/2	MPr(vr)
	Dune slack, HOLME, W. Norfolk, v.c. 28	53/709.448	2	Blown sand	7·2	1000	7/1	II(o)
cruenta	Fen, S.W. LOUGH CARRA, Ballinrobe, W. Mayo, v.c. H27	02/164.684	25	Carboniferous limestone	7·8	150	6/1–6/2	FF(r)
	Pavement, S. LOUGH GELAIN, Corrofin, Co. Clare, v.c. H9	11/314.944	35	Carboniferous limestone	7·3	100	6/2	FF(o)
	Fen, E. LOUGH BUNNY, Gort, Co. Clare, v.c. H9	11/382.975	20	Peat/Carboniferous limestone	7·7	150	6/2	FF(f)
pulchella	Marsh, EAST WALTON Common, W. Norfolk, v.c. 28	53/735.165	15	Peat/marine clay & sand/chalk	6.0^3	35	6/1–2	II(vr) FF(o) MPr(vr)
	Bog, THURSLEY Common, Surrey, v.c. 17	41/904.416	55	Peat/Lower greensand	6·0^3	1000	6/2	McE(r)
	Bog, N. of STEPHILL BOTTOM, Beaulieu, S. Hants., v.c. 11	41/360.061	20	Peat/Barton sand	4·5^3	100	6/1	McE(r)
	Bog, BAGSHOT Moor, east Boldre, S. Hants., v.c. 11	41/368.000	35	Peat/Plateau gravel	4·9^3	100	6/2–3	McE(vr)
	WICKEN Fen, Cambs., v.c. 29	52/556.701	6	Peat/Gault clay	7·6^3	9	6/2	II(f) IP(f)
ochroleuca	CHIPPENHAM Fen, Cambs., v.c. 29	52/6—.6—	12	Peat/chalk	7·7	50	6/1	II(vr) MPr(f)

13. Contrast of markings with base colour, on a scale 0–3 (0=no markings; 1=pale; 2=well-defined; 3=bold).
14. Indentations on right lateral lobe, on a scale 0–2 (0=none; 1=one notch; 2=more than one notch).

B. *Spur* (4 characters).

All except character 18 were taken from flattened mounted spurs.

15. Length, from entrance to apex.
16. Width, at entrance.
17. Width, halfway along length.
18. Curvature, on a scale 1–5 (1=strongly recurved through to 5=strongly decurved).

C. *Lateral outer perianth segments* (3 characters).

19. Position relative to the median outer perianth segment, on a scale 1–5 (1=*c.* 100° through to 5=*c.* 10°).
20. Solid markings, on a scale 0–2 (0=none; 1=pale; 2=bold).
21. Annular markings, on a scale 0–2 (0=none; 1=pale; 2=bold).

D. *Bracts* (6 characters).

The size and shape of peripheral bract cells (characters 26 and 27) were examined at the suggestion of R. H. Roberts (pers. comm. 1980).

22. Length, basal bracts (base of infloresence).
23. Length, floral bracts (halfway up inflorescence).
24. Anthocyanin pigmentation, on a scale 0–2 (0=none; 1=diffuse; 2=heavy).
25. Presence (1) or absence (0) of markings.
26. Length of peripheral cells (mean of 10–30 cells).
27. Mean shape of peripheral cells, on a scale 1–3 (1=rounded, often barrel-shaped; 2=subangular; 3=angular).

E. *Stem and inflorescence* (6 characters).

28. Stature.
29. Inflorescence length.

30a. Ovary length.

31. Number of flowers.
32. Stem diameter, immediately above lowest sheathing leaf.
33. Stem anthocyanin immediately below inflorescence, on a scale 0–2 (0=none; 1=diffuse; 2=heavy).

F. *Leaves* (12 characters).

Three measurements were taken from each sheathing leaf: (i) length, (ii) maximum width, (iii) position of maximum width relative to length, on a scale 1–4 (1=0–10% of length; 2=10–25%; 3=25–50%; 4=>50%). These characters could not be compared directly as the number of sheathing leaves per plant varied. They were therefore summarised as characters 37–42.

FOOTNOTES TO TABLE 2

[1] The number before the oblique denotes the month, number(s) after the weeks of that month. Observations were made in 1981 (subsp. *cruenta*) and 1982 (all other subspecies), both particularly early seasons.

[2] FF=*D. fuchsii* subsp. *fuchsii*
McE=*D. maculata* subsp. *ericetorum*
II=*D. incarnata* subsp. *incarnata*
IP=*D. incarnata* subsp. *pulchella*
MP=*D. majalis* subsp. *purpurella*
MPr=*D. majalis* subsp. *praetermissa*
MT=*D. majalis* subsp. *traunsteinerioides*
'c'=common, 'f'=frequent, 'o'=occasional, 'r'=rare, 'vr'=very rare.

[3] Value approximate due to very large amount of organic matter in sample.

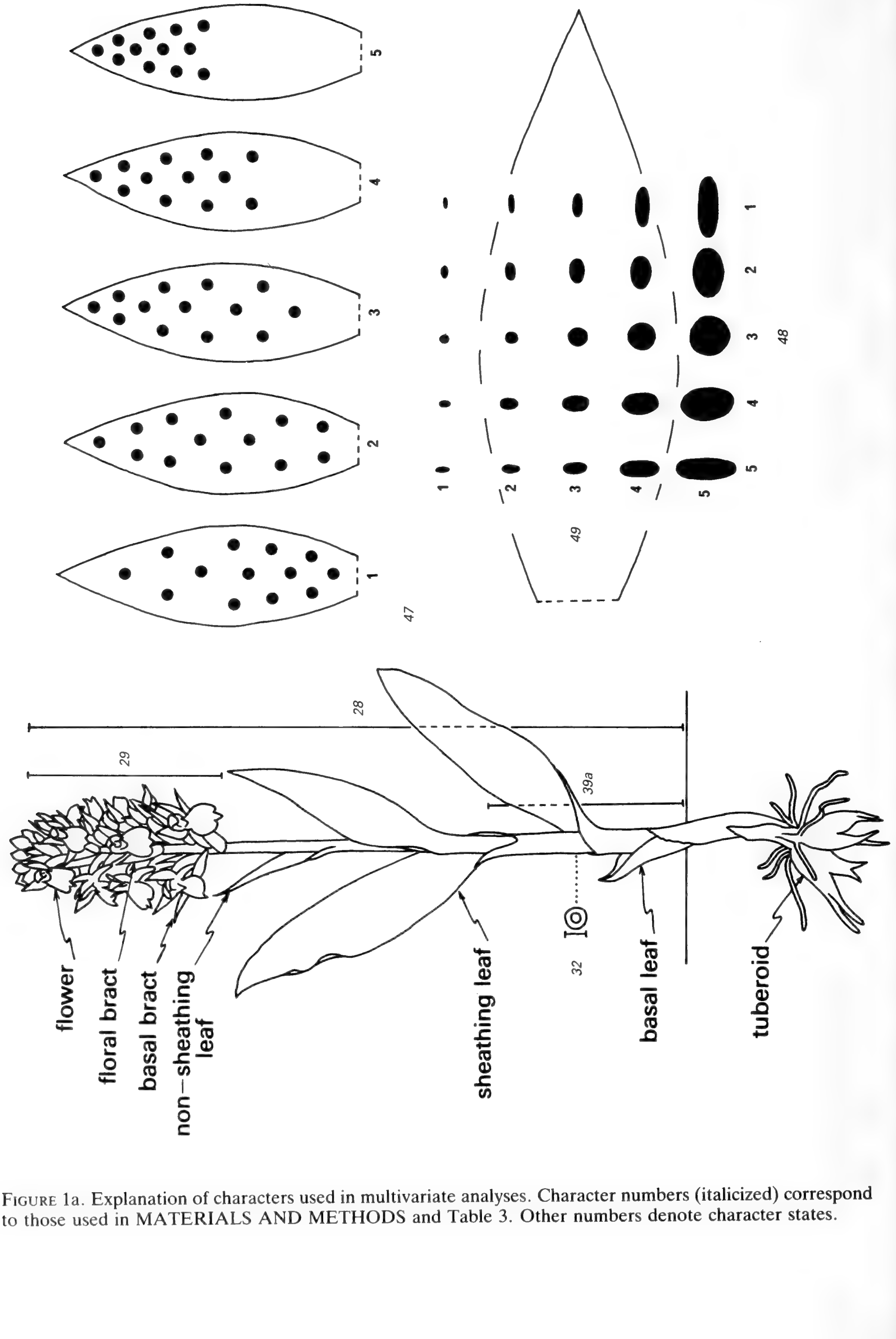


FIGURE 1a. Explanation of characters used in multivariate analyses. Character numbers (italicized) correspond to those used in MATERIALS AND METHODS and Table 3. Other numbers denote character states.

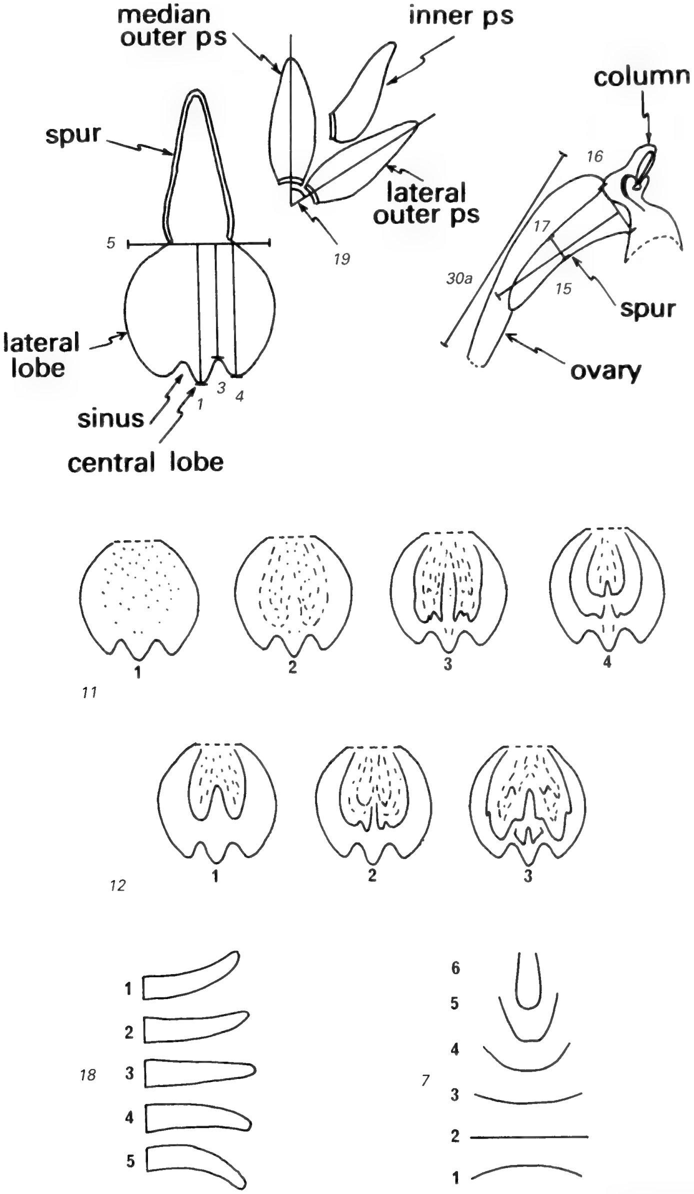


FIGURE 1b. Explanation of characters used in multivariate analyses. Character numbers (italicized) correspond to those used in MATERIALS AND METHODS and Table 3. Other numbers denote character states. ps=perianth segment.

34. Number of sheathing leaves (excluding basal leaf if present).
35. Number of non-sheathing leaves.
36. Presence (1) or absence (0) of a basal leaf. This is defined as ranging from a chlorophyllose sheath above ground level to a leaf up to half the length of the sheathing leaf immediately above.
37. Length of longest sheathing leaf.
38. Maximum width of widest sheathing leaf (width of longest leaf was also recorded if it was not the widest).

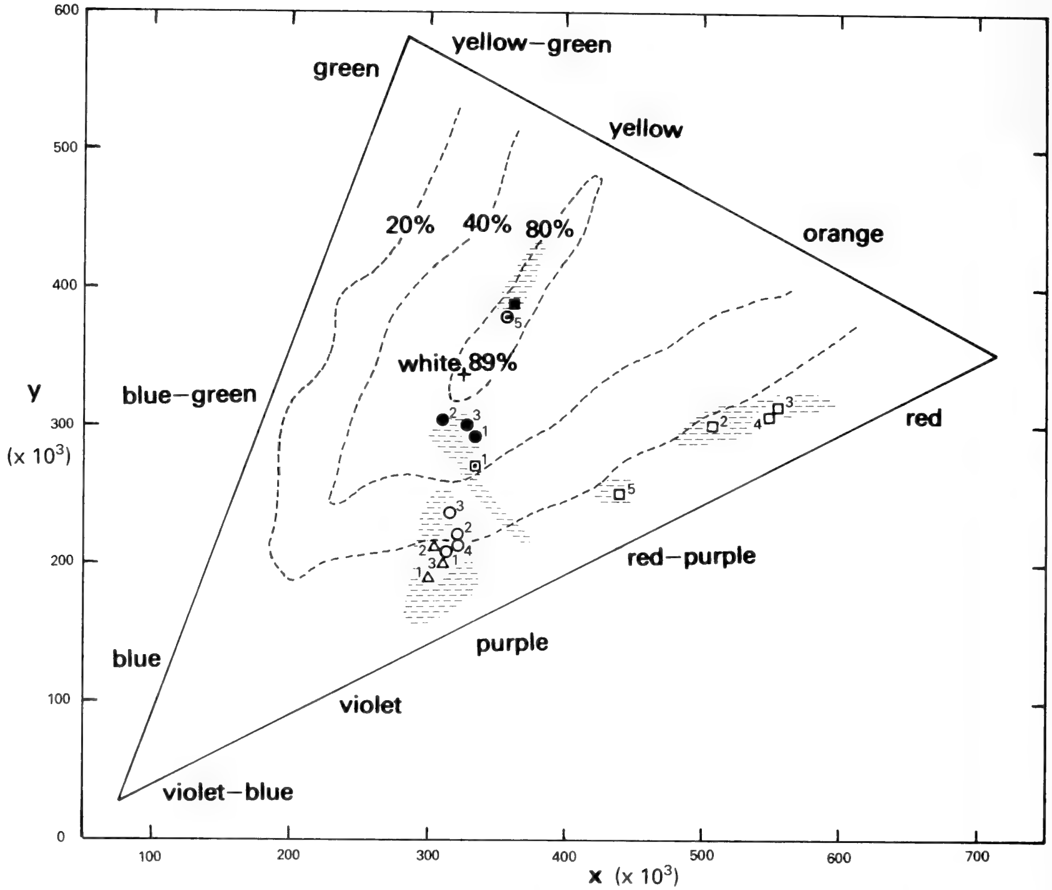


FIGURE 2. Variation of labellum colour in *D. incarnata*. An approximation of the C.I.E. colour triangle, derived from coordinates given in the R.H.S. Colour Chart (see MATERIALS AND METHODS). Dashed lines represent reflectivity contours. Hatched areas include points for all individual plants, symbols denote population means. The following symbols are used throughout the figures:
● subsp. *incarnata*
□ subsp. *coccinea* (⊡ Rhos-y-gad population)
△ subsp. *cruenta* (◬ leaf-marked individuals)
○ subsp. *pulchella* (⊙ Wicken population)
■ subsp. *ochroleuca*
Superscripts denote populations (shown in full in Fig. 5).

39. Relative positions of longest and widest sheathing leaves along stem, on a scale 1–3 (1=longest above widest; 2=longest is widest; 3=longest below widest).
39a. Height of base of longest leaf above ground level.
40. Shape of uppermost sheathing leaf (for details of shape index see [iii] above).
41. Shape of longest sheathing leaf.
42. Shape of lowest sheathing leaf (excluding basal leaf).
43. Hooding of apex of longest sheathing leaf, on a scale 0–2 (0=none; 1=poorly-defined; 2=well-defined).
44. Colour of longest sheathing leaf, on a scale 1–3 (1=yellow-green; 2=bright green; 3=dark green).

G. *Leaf markings* (7 characters).

Characters 46–51 were taken from the longest sheathing leaf.

45. Presence (1) or absence (0) of markings on any leaf.
46. Area of upper surface covered.
47. Distribution on upper surface, on a scale 1–5 (1=slightly concentrated towards base through to 5=extremely concentrated towards apex).
48. Mean shape, on a scale 1–5 (1=strongly longitudinally elongated through to 5=strongly transversely elongated).
49. Mean diameter, on a scale 1–5 (1=*c.* 1mm; 2=*c.* 1·5mm; 3=*c.* 2·5mm; 4=*c.* 4mm; 5=*c.* 6mm).
50. Proportion of annular markings (i.e. with green or very pale purple/brown centres), on a scale 0–2 (0=none; 1=<25% of total markings; 2=>25% of total markings).
51. Area of lower surface covered.

Some of the above characters were used to calculate the following ten indices, which summarise the shapes of certain structures. The characters are numbered according to the above list and preceded by the letter 'C':

a. Roundness of labellum. C1/(C1+C5).
b. Labellum shape index of Heslop-Harrison (1948) (if sinuses present). 2×C1/(C3+C4).
c. Prominence of central lobe (if sinuses present). C1−C4.
d. Tapering of spur. C17/(C17+C16).
e. Percentage of stem bearing flowers. 100×C29/C28.
f. Laxity of inflorescence (fls/cm). C31/C29.
g. Shape of longest leaf. Width of longest lf/(width of longest lf+C37).
h. Percentage of stem below base of longest leaf. 100×C39a/C28.
i. Ovary length as a percentage of floral bract length. 100×C30a/C23.
j. Spur length as a percentage of ovary length. 100×C15/C30a.

Data were analyzed by multivariate methods using the Genstat computer program (Alvey *et al.* 1977). Characters 3–4 (labellum dimensions) and 46–51 (details of leaf markings) were excluded from the multivariate analyses to avoid bias caused by series of zero values resulting from the absence of a single feature (i.e. labellum sinuses or leaf markings respectively). The 44 remaining characters were used to compute two symmetrical matrices of indices that quantified the similarities of pairs of data sets using Gower's (1971) coefficient of similarity:

$$S_{ij}=1-\frac{\sum_{k=1}^{pl} X_{ik}-X_{jk}}{pl}$$

where S_{ij} is the similarity between samples i and j in variate k, X_{ik} is the adjusted value for variate k in sample i, and pl is the total number of variates. The first matrix used population means, which were then linked by maximum similarities to yield a minimum spanning tree expressing their phenetic relationships (Gower & Ross 1969). The second similarity matrix was produced from data for individual plants and was used to calculate principal coordinates (Gower 1966; Blackith & Reyment 1971; Sneath & Sokal 1973), compound vectors incorporating positively or negatively correlated characters that are most variable and therefore of potential diagnostic value. The first two principal coordinates (PC1, PC2) were plotted together to assess the degree of morphological separation of taxa in these dimensions.

VARIATION IN SINGLE CHARACTERS

Population means for all recorded characters are listed in Table 3, with sample standard deviations where applicable.

TABLE 3. POPULATION MEANS (AND SAMPLE STANDARD DEVIATIONS IN PARENTHESES WHERE APPROPRIATE) OF RECORDED CHARACTERS

Character:	Labellum													
Population	1 mm	2	(3)[1] mm	(4) mm	5 mm	6	7	8 C.I.E. units	9 C.I.E. units	10 %	11	12	13	14
BLAGROVE	7·09 (0·54)	0·9	5·51 (0·52)	5·96 (0·65)	8·25 (0·47)	2·0	4·5	332·9 (5·1)	292·5 (11·7)	59·0 (7·9)	2·0	2·0	1·2	0
TRING	5·75 (0·64)	0·2	4·50 (0·57)	4·85 (0·49)	6·09 (0·63)	2·2	5·2	310·2 (3·8)	303·1 (3·5)	75·9 (3·5)	2·9	2·0	1·6	0·1
LLYN RHOS-DDU	5·79 (0·43)	0·9	4·58 (0·29)	5·06 (0·38)	7·11 (0·91)	1·8	5·5	328·2 (6·7)	299·4 (3·4)	64·0 (4·2)	3·0	1·2	1·6	0·4
RHOS-Y-GAD	5·36 (0·49)	0·6	4·25 (0·33)	4·68 (0·45)	6·27 (0·67)	2·0	4·8	333·8 (16·7)	267·4 (28·2)	46·8 (16·1)	3·4	2·0	2·1	0·2
NEWBOROUGH	4·93 (0·23)	0·7	3·96 (0·25)	4·26 (0·23)	5·51 (0·38)	2·3	5·3	508·5 (8·5)	300·4 (3·4)	12·8 (2·5)	3·0	2·0	1·8	0·4
MALLTRAETH	5·68 (0·42)	1·0	4·53 (0·44)	4·80 (0·44)	6·80 (0·46)	2·0	5·8	552·1 (12·1)	313·3 (5·9)	10·3 (2·4)	3·0	1·9	1·6	0·9
AINSDALE	6·09 (0·38)	0·7	5·01 (0·61)	5·53 (0·45)	7·92 (1·03)	2·2	4·7	542·3 (37·3)	310·9 (12·7)	13·3 (3·9)	3·1	2·1	2·0	0·7
HOLME	6·07 (0·34)	1·0	4·80 (0·36)	5·28 (0·33)	6·72 (0·45)	2·5	5·1	439·4 (5·1)	250·3 (0·9)	9·5 (1·6)	3·0	1·8	2·0	0·7
LOUGH CARRA	6·15 (0·40)	1·0	4·92 (0·53)	5·28 (0·74)	7·31 (0·90)	1·9	3·6	300·5 (13·6)	188·0 (24·1)	14·6 (5·2)	4·0	3·0	2·8	0·7
LOUGH GELAIN	6·96 (0·75)	0·8	5·63 (0·95)	5·91 (1·02)	8·00 (1·59)	1·9	3·5	306·5 (11·4)	213·4 (25·6)	20·3 (7·6)	3·5	2·6	1·9	0·3
LOUGH BUNNY	6·37 (0·58)	0·9	5·11 (1·03)	5·44 (0·94)	7·66 (1·14)	2·0	4·1	312·4 (12·0)	203·1 (23·3)	16·9 (6·1)	3·3	2·4	2·7	0·6
EAST WALTON	6·48 (0·29)	0·7	5·59 (0·27)	5·87 (0·28)	7·86 (0·34)	2·1	4·5	309·2 (1·0)	207·6 (16·0)	17·2 (3·6)	3·0	1·0	2·0	0·1
THURSLEY	5·75 (0·37)	0·4	4·70 (0·62)	4·95 (0·68)	6·45 (0·75)	2·3	5·4	318·6 (9·2)	223·0 (25·1)	22·2 (7·0)	3·3	2·0	2·4	0·5
STEPHILL	6·19 (0·76)	0·9	5·20 (0·83)	5·47 (0·82)	7·47 (1·10)	2·3	5·4	315·1 (2·8)	238·4 (42·7)	27·3 (11·4)	3·1	1·8	2·1	0·2
BAGSHOT	6·28 (0·41)	0·6	5·10 (0·51)	5·50 (0·49)	7·26 (0·42)	2·4	5·0	318·9 (9·0)	217·7 (44·5)	22·0 (12·8)	3·1	2·1	2·0	0·3
WICKEN	6·72 (0·61)	0·7	5·22 (0·44)	5·43 (0·43)	8·77 (0·63)	2·2	5·6	352·0 (0)	381·0 (0)	85·0 (0)	0	0	0	0·2
CHIPPENHAM	7·09 (1·00)	1·0	4·60 (0·93)	5·15 (0·96)	8·98 (0·81)	1·7	5·1	352·0 (0)	381·0 (0)	85·0 (0)	0	0	0	1·0

[1] Characters in parentheses were not used in multivariate analyses.

TABLE 3 (cont.) POPULATION MEANS (AND SAMPLE STANDARD DEVIATIONS IN PARENTHESES WHERE APPROPRIATE) OF RECORDED CHARACTERS

Character:	Spur				Lateral outer perianth segs.			Bracts					
Population	15 mm	16 mm	17 mm	18	19	20	21	22 mm	23 mm	24	25	26 μm	27
BLAGROVE	6·47 (0·59)	3·84 (0·20)	3·21 (0·16)	4·0	4·9	0·9	0	31·8 (4·5)	20·5 (2·7)	0	0	44·0 (5·8)	1·0
TRING	6·19 (0·40)	2·68 (0·30)	2·12 (0·15)	4·3	4·3	1·0	0·1	26·8 (7·1)	14·7 (3·1)	0	0	53·1 (5·7)	1·0
LLYN RHOS-DDU	7·16 (0·41)	3·34 (0·35)	2·46 (0·23)	4·5	4·8	1·1	0	21·7 (2·0)	14·9 (1·3)	0·4	0	48·8 (6·3)	1·1
RHOS-Y-GAD	6·44 (0·68)	2·60 (0·39)	1·97 (0·21)	4·4	4·7	1·1	0·9	15·3 (2·9)	11·3 (2·3)	1·5	0	46·4 (3·9)	1·1
NEWBOROUGH	6·10 (0·49)	3·08 (0·14)	2·73 (0·16)	4·4	4·9	0·8	0	14·3 (2·5)	10·6 (2·0)	1·8	0	46·1 (2·5)	1·5
MALLTRAETH	6·35 (0·44)	3·02 (0·25)	2·42 (0·20)	4·5	4·2	1·0	0	16·6 (2·1)	13·4 (1·3)	0·8	0	47·5 (7·2)	1·1
AINSDALE	6·92 (0·85)	3·70 (0·56)	2·85 (0·27)	4·7	5·0	0·7	0	18·6 (4·8)	13·7 (3·0)	1·6	0	46·9 (4·3)	1·7
HOLME	6·65 (0·63)	3·13 (0·25)	2·29 (0·24)	3·5	4·9	0·6	0·1	19·1 (2·3)	13·8 (2·4)	1·9	0	44·0 (6·9)	1·3
LOUGH CARRA	6·68 (0·69)	3·07 (0·48)	2·52 (0·27)	3·9	3·0	0·5	1·7	20·3 (3·2)	15·1 (1·9)	1·6	0·1	53·0 (8·4)	1·2
LOUGH GELAIN	6·74 (0·57)	3·28 (0·34)	2·71 (0·27)	4·2	2·4	1·2	1·2	21·7 (4·9)	15·7 (2·6)	1·5	0·3	52·2 (6·0)	1·1
LOUGH BUNNY	7·07 (0·70)	3·29 (0·37)	2·58 (0·35)	4·0	4·0	1·5	1·1	21·5 (2·9)	15·5 (1·7)	1·6	0	45·5 (3·1)	1·4
EAST WALTON	6·81 (0·26)	3·23 (0·18)	2·61 (0·17)	4·2	4·0	1·0	0	24·7 (1·3)	15·8 (1·6)	1·5	0	52·0 (6·6)	1·1
THURSLEY	5·88 (0·42)	3·12 (0·34)	2·47 (0·28)	4·5	3·1	1·7	1·9	19·3 (3·5)	13·1 (1·8)	0·6	0	58·7 (20·9)	1·1
STEPHILL	6·41 (0·98)	3·48 (0·54)	2·72 (0·50)	4·2	3·9	1·4	0·3	21·7 (4·7)	11·6 (3·1)	0·3	0	50·9 (6·5)	1·3
BAGSHOT	6·75 (0·78)	3·56 (0·28)	3·06 (0·12)	4·2	2·9	1·3	0·4	19·5 (3·7)	12·7 (2·3)	0·6	0	58·1 (7·0)	1·8
WICKEN	7·58 (0·36)	3·16 (0·26)	2·63 (0·27)	3·4	4·4	0	0	19·8 (3·3)	14·4 (1·8)	0	0	53·3 (7·1)	2·0
CHIPPENHAM	5·09 (1·89)	3·90 (0·71)	3·05 (0·13)	3·1	3·3	0	0	39·5 (8·3)	22·8 (4·5)	0	0	49·8 (5·9)	1·7

TABLE 3 (cont.) POPULATION MEANS (AND SAMPLE STANDARD DEVIATIONS IN PARENTHESES WHERE APPROPRIATE) OF RECORDED CHARACTERS

Character:	Stem and inflorescence						Leaves										
Population	28 cm	29 mm	30a mm	31	32 mm	33	34	35	36	37 mm	38 mm	39	39a cm	40	41	42	43	44
BLAGROVE	25·5 (5·5)	62·7 (20·4)	13·3 (1·5)	32·2 (10·0)	8·14 (1·23)	0	3·9	1·1	1·0	119·5 (14·0)	25·0 (4·6)	1·8	7·4	1·7	2·0	2·8	1·6	1·0
TRING	25·1 (9·6)	61·0 (19·2)	9·8 (1·8)	29·2 (9·5)	7·23 (1·00)	0	4·4	1·1	1·0	123·5 (19·5)	22·7 (2·3)	1·7	4·5	1·8	2·0	2·6	1·3	2·0
LLYN RHOS-DDU	31·2 (3·8)	71·4 (10·3)	10·3 (1·2)	27·6 (5·9)	6·58 (0·57)	0	4·3	1·5	0·9	102·3 (16·1)	26·5 (3·4)	1·6	6·6	1·7	2·2	2·7	1·2	1·9
RHOS-Y-GAD	18·2 (5·5)	32·9 (8·1)	9·0 (0·9)	13·1 (4·4)	3·84 (0·57)	1·1	3·9	0·7	0·3	75·7 (14·4)	12·3 (2·5)	2·1	3·6	1·4	2·1	2·8	1·4	1·2
NEWBOROUGH	9·9 (2·5)	35·9 (11·8)	9·8 (0·9)	11·7 (4·3)	3·13 (0·33)	0·6	3·6	0·5	1·0	47·1 (9·3)	12·4 (2·4)	1·8	0·5	1·7	2·1	2·4	1·2	1·0
MALLTRAETH	13·9 (2·1)	38·4 (5·7)	11·1 (0·9)	17·3 (5·4)	4·17 (0·85)	0·4	4·0	1·7	1·0	87·5 (12·2)	16·3 (3·2)	1·7	3·1	2·3	2·7	3·0	1·2	1·5
AINSDALE	10·7 (2·9)	47·6 (13·5)	11·3 (2·6)	28·2 (14·5)	5·29 (2·19)	0·4	4·0	1·1	1·0	73·9 (13·4)	19·7 (7·3)	1·7	1·2	1·8	2·1	2·6	0·9	1·4
HOLME	16·5 (7·4)	37·3 (8·5)	8·7 (1·3)	17·1 (6·7)	4·22 (0·78)	1·5	3·3	1·6	1·0	101·7 (24·0)	14·5 (2·1)	1·8	4·3	2·4	3·0	3·1	0·8	2·1
LOUGH CARRA	15·0 (2·5)	42·3 (7·2)	9·5 (1·0)	21·3 (6·0)	4·53 (0·92)	1·5	3·3	1·1	1·0	70·9 (24·2)	14·7 (3·8)	2·0	—	2·2	2·1	1·9	1·9	1·4
LOUGH GELAIN	15·9 (3·2)	37·6 (7·4)	10·0 (1·1)	13·8 (4·0)	4·02 (0·70)	1·1	3·6	1·0	1·0	93·0 (24·8)	12·5 (2·6)	2·0	—	1·9	1·7	1·9	1·7	1·5
LOUGH BUNNY	21·6 (4·0)	42·0 (5·3)	9·5 (0·8)	17·3 (2·5)	4·32 (0·70)	0·8	3·5	0·9	1·0	79·8 (12·5)	13·2 (3·0)	2·0	—	1·7	2·2	2·2	1·9	1·4
EAST WALTON	30·7 (5·1)	45·4 (9·1)	10·6 (1·0)	25·8 (6·5)	5·09 (0·76)	0·1	3·7	1·2	0·9	130·9 (19·4)	14·4 (2·3)	1·9	11·3	1·4	1·9	2·2	1·9	1·2
THURSLEY	23·5 (6·4)	49·0 (12·4)	9·5 (1·0)	23·3 (10·1)	5·05 (1·27)	0	2·9	0·8	0·4	105·0 (22·8)	13·3 (2·7)	1·9	6·6	1·7	2·0	2·6	1·1	1·7
STEPHILL	19·2 (4·0)	43·4 (15·5)	8·9 (1·9)	21·2 (10·0)	4·64 (2·10)	0	3·0	1·1	0·8	83·8 (24·0)	14·4 (3·8)	1·9	5·0	2·1	2·7	3·0	1·0	2·0
BAGSHOT	19·1 (3·2)	46·3 (10·0)	9·6 (1·1)	33·4 (6·4)	5·07 (0·91)	0	2·9	0·9	1·0	86·4 (9·4)	16·9 (2·3)	1·9	4·3	1·7	2·5	2·8	1·1	1·8
WICKEN	12·1 (3·7)	32·8 (8·5)	9·6 (1·6)	13·3 (3·1)	4·88 (1·12)	0	3·3	0·9	1·0	118·3 (18·4)	20·4 (3·2)	1·7	3·9	2·0	2·6	2·8	1·0	1·3
CHIPPENHAM	34·8 (9·6)	67·4 (20·0)	11·3 (1·7)	33·0 (13·0)	9·97 (2·01)	0	3·5	1·1	1·0	109·8 (14·8)	29·1 (4·1)	2·0	12·1	1·4	2·2	2·5	1·6	1·5

TABLE 3 (cont.) POPULATION MEANS (AND SAMPLE STANDARD DEVIATIONS IN PARENTHESES WHERE APPROPRIATE) OF RECORDED CHARACTERS

Character:	Leaf markings							Indices										
Population	45	(46)[1] %	(47)	(48)	(49)	(50)	51 %	(a)	(b)	(c) mm	(d)	(e) %	(f) fls/cm	(g)	(h) %	(i) %	(j) %
BLAGROVE	0	0	0	0	0	0	0	0·462	1·25	0·44	0·453	24·7	5·2	0·171	38·3	65·5	50·2
TRING	0	0	0	0	0	0	0	0·478	1·17	0·60	0·442	24·9	4·8	0·156	21·5	68·5	64·8
LLYN RHOS-DDU	0	0	0	0	0	0	0	0·451	1·21	0·76	0·425	23·0	4·0	0·203	27·7	69·7	70·5
RHOS-Y-GAD	0	0	0	0	0	0	0	0·461	1·14	0·42	0·433	18·7	4·0	0·139	22·9	82·5	72·0
NEWBOROUGH	0	0	0	0	0	0	0	0·423	1·21	0·70	0·469	35·8	3·3	0·207	6·7	94·5	62·8
MALLTRAETH	0	0	0	0	0	0	0	0·455	1·22	0·27	0·446	28·1	4·5	0·154	29·4	83·5	57·4
AINSDALE	0	0	0	0	0	0	0	0·436	1·18	0·59	0·431	45·2	5·7	0·207	16·2	84·4	62·9
HOLME	0	0	0	0	0	0	0	0·472	1·21	0·79	0·424	25·8	4·5	0·125	30·8	63·7	64·1
LOUGH CARRA	0·4	14·3	3·5	3·5	1·8	0	15·0	0·458	1·22	0·77	0·453	28·6	5·0	0·176	—	63·5	70·7
LOUGH GELAIN	0·3	8·3	3·0	3·0	2·3	0	10·0	0·469	1·24	1·16	0·451	23·5	3·7	0·121	—	62·2	74·6
LOUGH BUNNY	0·2	11·0	1·0	2·5	1·0	0	0	0·456	1·25	0·96	0·440	19·8	4·2	0·143	—	65·0	71·1
EAST WALTON	0	0	0	0	0	0	0	0·452	1·13	0·29	0·449	15·3	5·7	0·099	42·2	67·8	64·7
THURSLEY	0	0	0	0	0	0	0	0·473	1·21	0·83	0·443	21·7	4·6	0·115	36·0	74·0	62·4
STEPHILL	0	0	0	0	0	0	0	0·453	1·17	0·76	0·438	24·0	4·8	0·150	33·0	79·5	70·7
BAGSHOT	0	0	0	0	0	0	0	0·463	1·19	0·80	0·464	24·7	7·3	0·160	28·3	76·6	70·9
WICKEN	0	0	0	0	0	0	0	0·434	1·22	1·03	0·454	28·7	4·1	0·146	46·6	67·3	80·6
CHIPPENHAM	0	0	0	0	0	0	0	0·438	1·48	1·94	0·425	20·2	4·9	0·210	43·8	51·5	44·1

[1] Characters in parentheses were not used in multivariate analyses.

TABLE 4. FLORAL PIGMENTATION SCHEMES FOR THE SUBSPECIES OF *D. INCARNATA*
a) Scheme suggested by observations of Heslop-Harrison (1956).
b) Scheme suggested by observations of Uphoff (1979, 1982) and the present authors.

a) Subspecies	Purple anthocyanin Intense	Purple anthocyanin Dilute	Yellow anthoxanthin (acting as co-pigment)
pulchella	+	−	−
cruenta	+	−	−?
coccinea	+	−	+
incarnata	−	+	+
ochroleuca	−	−	+

b) Subspecies	red anthocyanins[1]	Violet anthocyanin[2]	Yellow anthoxanthin	Combined density of pigments (measured as % reflectivity)
pulchella	+	+	+	dark/moderate
cruenta	+	+	+	dark/moderate
coccinea	+	−	+	dark/moderate/(pale)
incarnata	+	−	+	pale
ochroleuca	−	−	+	very pale

[1] Cyanin (no co-pigment) and Orchicyanin II (cyanin with a non-bathochromic co-pigment).
[2] Orchicyanin I (cyanin with a bathochromic co-pigment).

PIGMENTATION CHARACTERS

The characters showing most variation between subspecies of *D. incarnata* are those determined by the presence and distribution of floral pigments. Consequently, flower colour is the major diagnostic character of the subspecies given in *Flora Europaea* (Soó 1980), and is the only criterion used to distinguish the subspecies in some other treatments. Fig. 2 illustrates the variation in flower colour found in each of the subspecies examined during the present study. Yellow-flowered plants formed a cohesive group, which occurred within the 80% reflectivity contour but was distinct from the maximum (89%) reflectivity point that represents pure white. This group comprised the Chippenham population of *D. incarnata* subsp. *ochroleuca*, the Wicken sample (thought to be anthocyanin-less subsp. *pulchella*), and six pale yellow-flowered plants that were included in samples of subsp. *pulchella* from Thursley, Stephill and Bagshot.

D. incarnata subsp. *incarnata* formed a cohesive group between the 40% and 80% reflectivity contours. The exceptionally variable Rhos-y-gad population of *D. incarnata* subsp. *coccinea* spanned both the 20% and 40% reflectivity contours and overlapped with subsp. *incarnata* on the colour triangle. Flowers of plants from Rhos-y-gad also had an appreciable purple-violet component, and were consequently separated from the other dark (reflectivity <20%), predominantly red-flowered populations of subsp. *coccinea*. We have examined populations of *D. incarnata* subsp. *coccinea* that are intermediate in flower colour to the red-purple-flowered Rhos-y-gad population and the main groups of red-flowered populations in Fig. 2. However, although the Rhos-y-gad population was atypical in flower colour, it resembled the other populations of *D. incarnata* subsp. *coccinea* in most characters (Table 3).

D. incarnata subsp. *cruenta* and subsp. *pulchella* both occupied the violet-purple colour zone and showed almost complete overlap in Fig. 2. These subspecies had flower colours that were either dark (reflectivity <20%) or, less frequently, moderate (20%–40%).

Labellum colours of diploid marsh-orchids can thus be resolved into three groups: red/red-purple (*D. incarnata* subsp. *incarnata* and subsp. *coccinea*), purple/purple-violet (subsp. *cruenta* and subsp. *pulchella*), and yellow (subsp. *ochroleuca* and anthocyanin-less variants of other subspecies). Heslop-Harrison (1956) also recognized these three groups and devised a pigmentation scheme to account for them (Table 4a). He postulated that all the subspecies of *D. incarnata* except subsp. *ochroleuca* contain a purple anthocyanin, which is modified to red in subsp. *incarnata* and subsp. *coccinea* by a yellow anthoxanthin that acts as a co-pigment. Flowers of *D. incarnata* subsp. *ochroleuca* contain only the yellow anthoxanthin, which is masked by anthocyanin in other subspecies and evident only in anthocyanin-less variants (often incorrectly described as albinos). Anthocyanin-less plants of *D. incarnata* subsp. *incarnata* and subsp. *coccinea* should therefore be yellow and those of subsp. *pulchella* and subsp. *cruenta* should be white (i.e. true albinos, lacking all floral pigments) if Heslop-Harrison's scheme is correct.

Flowers of anthocyanin-less plants of *D. incarnata* subsp. *incarnata* and subsp. *coccinea* are indeed yellow (Clarke 1882; Heslop-Harrison 1956), but so are those of subsp. *pulchella* and subsp. *cruenta*. Anthocyanin-less individuals of *D. incarnata* subsp. *pulchella* occurred in four of the five populations that we examined (Stephill, 50% of the population; Bagshot, 30%; Wicken, 5%; Thursley, 1%), but their flowers were without exception suffused with yellow anthoxanthin. We have seen several pale yellow-flowered individuals of *D. incarnata* subsp. *cruenta* at Lough Carra, and Landwehr (1977) illustrated a yellow-flowered individual of this subspecies from Europe. True albinos of *D. incarnata*, presumably the result of non-expression of genes coding for both anthocyanins and anthoxanthins, appear to be very rare. Yellow anthoxanthin is evidently ubiquitous in *D. incarnata*, and therefore cannot be the cause of the red flower colour of subsp. *incarnata* and subsp. *coccinea*.

Chromatographic investigations by Uphoff (1979, 1982) suggest a more probable pigmentation scheme for *D. incarnata* (Table 4b). Flowers of *D. fuchsii* (Druce) Soó, *D. maculata* (L.) Soó, *D. majalis* (Reichenbach) P. F. Hunt & Summerhayes and *D. sambucina* (L.) Soó contain *c.* 10% red Cyanin, 25% red Orchicyanin II (Cyanin plus a non-bathochromic co-pigment) and 65% violet Orchicyanin I (Cyanin plus a bathochromic co-pigment). The synthesis of the co-pigment occurs during anthesis, causing a bathochromic shift in maximum absorbance that is expressed as a change in flower colour from red to purple-violet (Uphoff 1982). Similar colour changes occur during anthesis in flowers of *D. incarnata* subsp. *cruenta* and subsp. *pulchella*, which probably contain Orchicyanin I. The red flowers of *D. incarnata* subsp. *coccinea* and subsp. *incarnata* presumably contain only Cyanin and Orchicyanin II, though some Orchicyanin I may be present in the red-purple-flowered populations of subsp. *coccinea* at Holme and, especially, Rhos-y-gad.

Uphoff (1979) also demonstrated large differences in the total amount of anthocyanins both within and between species of *Dactylorhiza*. We measured density of pigment indirectly, using percentage reflectivity to define four categories: dark, reflectivity 8–20%; moderate, 20–40%; pale, 41–80%; very pale, 81–89%. Flowers of *D. incarnata* subspp. *cruenta, pulchella* and *coccinea* are predominantly dark, though flowers of subsp. *cruenta* and subsp. *pulchella* are occasionally moderate and those of subsp. *coccinea* are rarely moderate or pale (Fig. 2, Table 4b). Flowers of *D. incarnata* subsp. *incarnata* are pale (reflectivity <55% in all the plants that we examined), and those of subsp. *ochroleuca* and anthocyanin-less variants of other subspecies are very pale. *D. incarnata* subsp. *incarnata* and subsp. *coccinea* probably contain the same combination of anthocyanins, though they are much more concentrated in most individuals of subsp. *coccinea*.

The presence and distribution of anthocyanins also determine characters that describe markings on labella, lateral outer perianth segments, leaves and bracts, and also diffuse bract and stem pigmentation, so these characters are not expressed by *D. incarnata* subsp. *ochroleuca*. *D. incarnata* subsp. *cruenta* is characterized by bold, broad labellum markings that are deficient in dashes and often cover most of the labellum. *D. incarnata* subspp. *pulchella, coccinea* and *incarnata* usually have less distinct loop markings that enclose dashes and cover less than two-thirds of the labellum.

Lateral outer perianth segment markings are usually solid in *D. incarnata* subsp. *incarnata* and subsp. *coccinea*, but are occasionally annular in subsp. *pulchella* and often annular in subsp. *cruenta*. *D. incarnata* subspp. *coccinea*, *cruenta* and *pulchella* frequently have anthocyanin pigmentation on the bracts, which often extends to the upper part of the stem in subsp. *cruenta* and subsp. *coccinea*. Vegetative anthocyanins are reddish-brown in *D. incarnata* subsp. *coccinea* but purplish-brown in subsp. *cruenta* and subsp. *pulchella*. Leaf and bract markings are virtually restricted to some individuals of *D. incarnata* subsp. *cruenta*, and occur independently of variation in other pigmentation characters such as density (i.e. reflectivity) of flower colour and boldness of labellum markings.

TABLE 5. VARIATES CONTRIBUTING APPRECIABLY TO THE FIRST TWO PRINCIPAL COORDINATES, LISTED IN ORDER OF DECREASING IMPORTANCE. ANALYSIS INCLUDES FLORAL PIGMENTATION CHARACTERS

Principal coordinate		PC1			PC2	
Percentage of variance accounted for		23·9%			10·7%	
Taxonomic significance of coordinate[1]		*ochroleuca*+anthocyanin-less *pulchella*: *incarnata*: *coccinea*+*pulchella*. *cruenta*			anthocyanin-less *pulchella*: *ochroleuca*, also *coccinea*: remainder	
Variate number, variate name, and direction of increase in value of variate in relation to increase in value of vector (e.g. individuals with more conspicuous labellum markings tend to occur towards the right side of PC1 on Fig. 3, whereas plants with pale-coloured labella tend to occur towards the left side).	11	Labellum markings, type	+	8	Labellum colour, ‘x’	−
	10	Labellum colour, reflectivity (Y)	−	39a	Position of longest leaf up stem	+
	13	Labellum markings, contrast	+	19	L.o.p.s., position	−
	9	Labellum colour, ‘y’	−	21	L.o.p.s., annular markings	+
	24	Bract anthocyanin	+	23	Length of floral bracts	+
	12	Labellum markings, distribution	+	28	Plant height	+
	38	Width of widest leaf	−	22	Length of basal bracts	+
	32	Stem diameter	−	43	Hooding of leaf tips	+
	33	Stem anthocyanin	+	7	Labellum lateral lobe reflexion	−
	22	Length of basal bracts	−	1	Labellum, length to central lobe	+
	21	L.o.p.s.[2], annular markings	+			
	37	Length of longest leaf	−			
	23	Length of floral bracts	+			
	20	L.o.p.s., solid markings	−			

[1] Stop indicates partial separation, colon indicates more-or-less complete separation.
[2] L.o.p.s.=lateral outer perianth segments.

TABLE 6. VARIATES CONTRIBUTING APPRECIABLY TO THE FIRST TWO PRINCIPAL COORDINATES, LISTED IN ORDER OF DECREASING IMPORTANCE. ANALYSIS EXCLUDES FLORAL PIGMENTATION CHARACTERS

Principal coordinate	PC1			PC2		
Percentage of variance accounted for	18·4%			12·5%		
Taxonomic significance of coordinate[1]	*ochroleuca*: anthocyanin-less *pulchella*. *incarnata*. *coccinea*+*pulchella*. *cruenta*			*ochroleuca*+*cruenta*. remainder		
Variate number, variate name, and direction of increase in value of variate in relation to increase in value of vector (see Table 5).	24	Bract anthocyanin	+	2	Presence of labellum sinuses	–
	32	Stem diameter	–	5	Labellum, width	+
	38	Width of widest leaf	–	39a	Position of longest leaf up stem	+
	22	Length of basal bracts	–	7	Labellum lateral lobe reflexion	–
	33	Stem anthocyanin	+	18	Spur curvature	–
	29	Inflorescence length	–	1	Labellum, length to central lobe	+
	31	Number of flowers	–	23	Length of floral bracts	+
	23	Length of floral bracts	–	33	Stem anthocyanin	+
	37	Length of longest leaf	–			
	28	Plant height	–			

[1] Stop indicates partial separation, colon indicates more-or-less complete separation.

OTHER CHARACTERS

D. incarnata is said to have entire or sub-entire labella (Summerhayes 1951; Clapham 1962; Soó 1980), but most plants in the majority of populations that we studied possessed labellum sinuses (Table 3). Furthermore, the strong reflexion of the lateral lobes that is said to characterize labella of *D. incarnata* is not always evident, particularly in subsp. *cruenta*, and the supposedly upright lateral outer perianth segments are often nearer horizontal in subspp. *cruenta*, *pulchella* and *ochroleuca*. Spurs of *D. incarnata* are usually broad and fairly long. Soó's (1980) statement that the spur is less than half the length of the ovary was true of only 7% of the plants that we examined. Sundermann (1975) used spur length/ovary length (our index 'j') to differentiate subspecies of *D. incarnata*, but our populations showed little variation in this ratio (Table 3).

Leaves of *D. incarnata* are fairly constant in number but variable in size and shape. *D. incarnata* subsp. *incarnata* and subsp. *ochroleuca* have relatively tall, broad stems, long many-flowered inflorescences and are generally the most vigorous subspecies. They also have large bracts; even the floral bracts of subsp. *ochroleuca* often considerably exceed the flowers. Their leaves are large and particularly broad (index 'g' values >0·2, Table 3), suggesting that leaf width is a useful diagnostic character for *D. incarnata* subsp. *incarnata* and subsp. *ochroleuca*, though Heslop-Harrison (1956) obtained narrower mean leaf widths for populations of these subspecies. Only 50% of all the plants that we measured had yellow-green leaves and only 41% had leaves with strongly hooded (cucculate) tips, features that supposedly characterize *D. incarnata* (Summerhayes 1951; Clapham 1962; Soó 1980). The peripheral bract cells of all subspecies of *D. incarnata* are small and generally rounded.

MULTIVARIATE ANALYSES AND TAXONOMIC STATUS

33 of the 44 characters used for multivariate analyses contributed appreciably to the first two principal coordinates (Table 5). The first principal coordinate (PC1 on Fig. 3) accounted for 23·9% of the total variance, and partially separated individuals into four groups comprising subsp. *incarnata*, subspp. *coccinea* and *pulchella*, subsp. *cruenta*, and plants lacking anthocyanins. Although PC2 was weaker, accounting for only 10·7% of the variance, it partially separated *D. incarnata* subsp. *ochroleuca* from other plants lacking anthocyanins, and subsp. *coccinea* from subsp. *pulchella*. PC1 and PC2 together resolved individuals into six groups (Fig. 3); five corresponded to subspecies recognized by Heslop-Harrison (1954, 1956), the sixth comprised anthocyanin-less plants that showed only minimal overlap with *D. incarnata* subsp. *ochroleuca*. There was a marked discontinuity between plants with anthocyanins and those without.

The six characters contributing most to PC1 and two of the four most important contributors to PC2 were determined by the presence and/or density of anthocyanins (Table 5). This resulted in the scattered distribution on Fig. 3 of Rhos-y-gad plants of *D. incarnata* subsp. *coccinea*, which were unusually variable in flower colour. When anthocyanin-dependent floral characters (nos. 8–13, 20–21) were omitted from principal coordinates analyses, the six groups evident in Fig. 3 were much less cohesive and their overlap increased considerably (Fig. 4), illustrating the importance of these characters for separating subspecies of *D. incarnata*. Much of the remaining separation reflected variation in characters describing vegetative anthocyanins, plant size and vigour, and the depth of labellum sinuses (Table 6). The Chippenham population of *D. incarnata* subsp. *ochroleuca* persisted as a separate cohesive group because of its vegetative vigour and large, deeply three-lobed labella, but other anthocyanin-less plants were separated from subsp. *ochroleuca* and occurred in the zone of overlap of subsp. *incarnata* and subsp. *pulchella*. The close affinity of Rhos-y-gad to other populations of *D. incarnata* subsp. *coccinea* is more apparent on this second plot (Fig. 4).

Minimum spanning trees of population means supported these taxonomic relationships (Fig. 5). In the tree incorporating floral pigmentation characters (Fig. 5a), the weakest links (i.e. lowest maximum similarities) occurred between the Chippenham population of *D. incarnata* subsp. *ochroleuca* and subsp. *incarnata*, and between subsp. *incarnata* and subsp. *pulchella*. The sample of anthocyanin-less plants from Wicken was loosely attached to the Stephill population of *D. incarnata* subsp. *pulchella* and had a very low similarity (78·8%) to the Chippenham population of

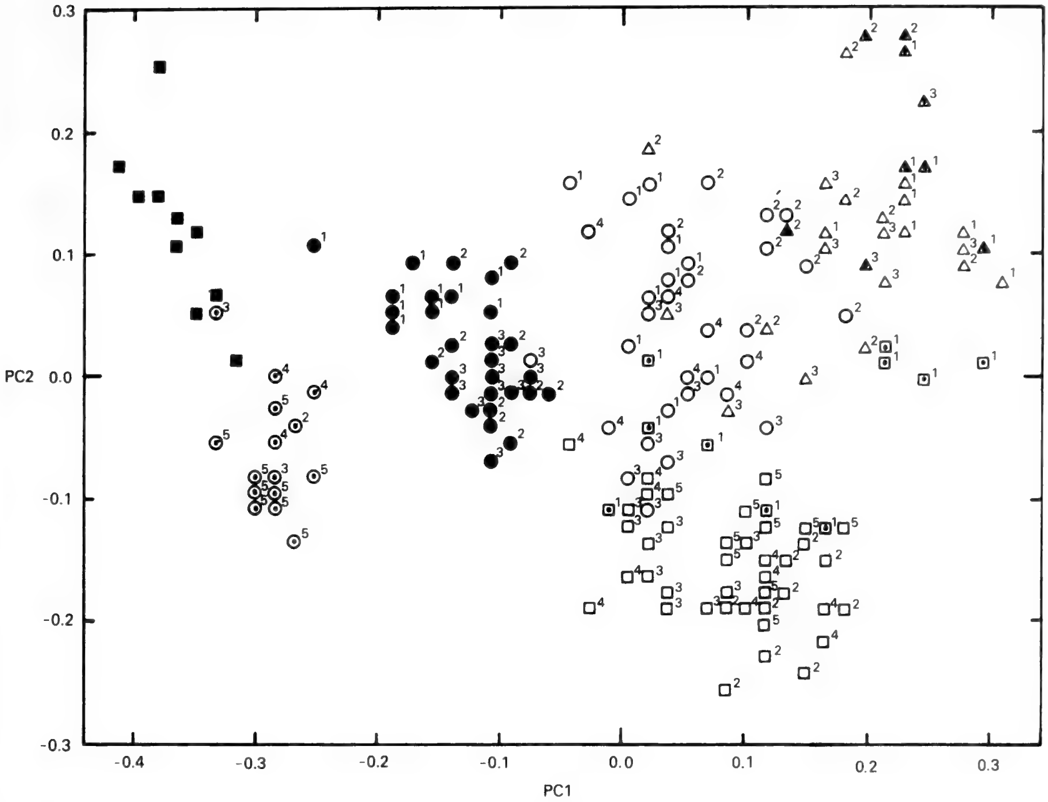


FIGURE 3. Principal Coordinates plot of PC1:PC2 for individual plants. Analysis includes floral pigmentation characters.
See Fig. 2 for explanation of symbols.

subsp. *ochroleuca*. The very cohesive group of *D. incarnata* subsp. *cruenta* populations surprisingly also included the East Walton population of subsp. *pulchella*, showing that the maximum similarities of populations of different subspecies can be greater than those of populations of the same subspecies. In the tree excluding anthocyanin-dependent floral characters (Fig. 5b), subsp. *incarnata* was loosely connected to subsp.*coccinea* (including the Rhos-y-gad population) rather than subsp. *pulchella*. The link between the sample of anthocyanin-less plants from Wicken and subsp. *pulchella* was strengthened, suggesting that the Wicken plants should be referred to this taxon rather than to subsp. *ochroleuca*.

We argued in an earlier paper (Bateman & Denholm 1983a) that the four British and Irish tetraploid marsh-orchid taxa formerly regarded as species merited only subspecific status because they showed mutual and approximately equal overlap on principal coordinates plots. The amount of separation of the diploid marsh-orchids was less consistent (Figs 3 & 4); the subspecies showed varying degrees of overlap on the plots. However, the discontinuities evident between some subspecies in Fig. 3 were largely due to variations in floral pigmentation characters, which must be interpreted with caution since they may reflect pleiotropism of few genes. Nevertheless, we consider that these colour differences, the partial morphological differentiation apparent even when pigmentation characters were excluded (Fig. 4), and some ecological specialization (see 'Evolutionary Aspects'), together justify the retention of these taxa as subspecies, though they are recognizable primarily by differences in population means for only a few characters. Other published data (Heslop-Harrison 1956) show that some of the subspecies are more variable than our results suggest and are unlikely to be separated by morphological discontinuities. The purple-

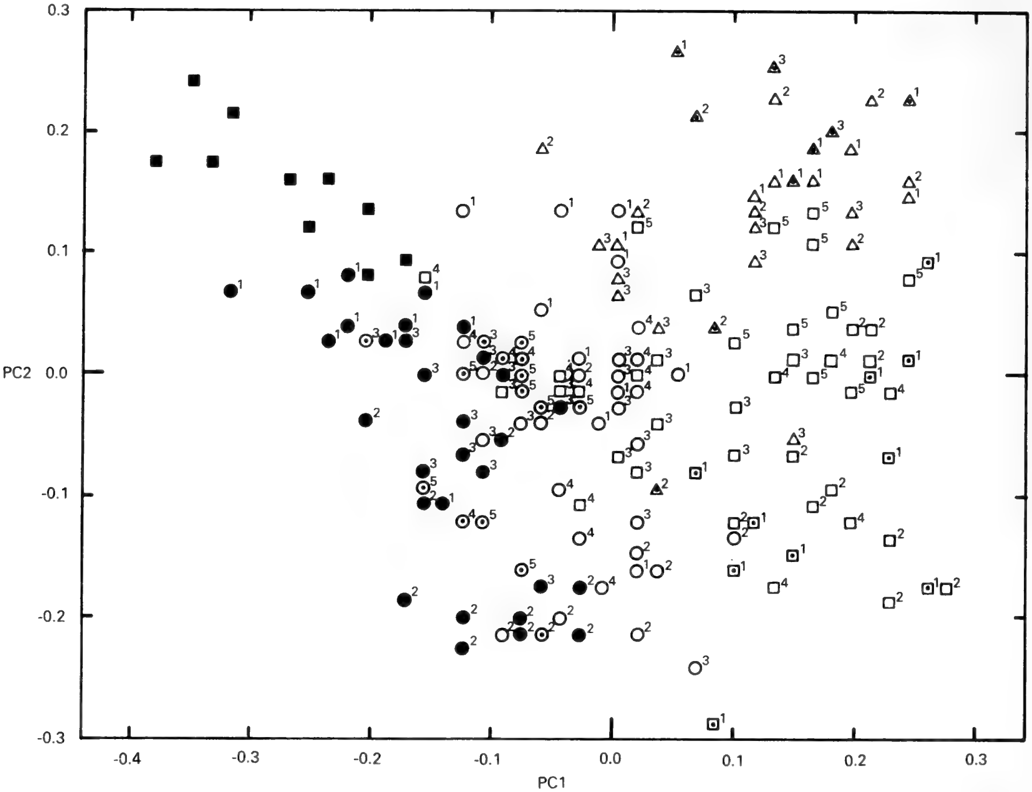


FIGURE 4. Principal Coordinates plot of PC1:PC2 for individual plants. Analysis excludes floral pigmentation characters.
See Fig. 2 for explanation of symbols.

flowered *D. incarnata* subsp. *pulchella* and subsp. *cruenta* pose the greatest taxonomic problems; they share the same range of purple/purple-violet flower colour (Fig. 2) and overlap considerably on the principal coordinates plots. Consequently, the identity of some populations, particularly in western Ireland, has been controversial (see 'Classification').

Our analyses suggest that *ochroleuca* is the most distinct subspecies of *D. incarnata*; further study may show that it merits specific rank. Unfortunately, it has become so rare in Britain that such work will need to be performed on Continental material.

EVOLUTIONARY ASPECTS OF VARIATION IN *D. INCARNATA*

The causes of the extensive variation within and between populations of *D. incarnata* are poorly understood. Small-scale experiments using different cultivation regimes showed that many floral characters of this species are probably under direct genetic control (Heslop-Harrison 1956). However, vegetative characters, which are generally more subsceptible than floral characters to environmental modification (Clausen *et al.* 1940; Heslop-Harrison 1953; Cook 1968; Jones & Luchsinger 1979), have not been examined in this way. Until more is known of the relative contributions of genotype and environment to this variation, both the extent of evolutionary divergence of the subspecies and the adaptive significance of the differences between them must remain speculative. Any genetic differentiation that does exist could only be maintained if one or more possible barriers to gene flow between subspecies prevents (or restricts) their hybridization. Most of the potential barriers to gene exchange listed by Stace (1975) are considered below.

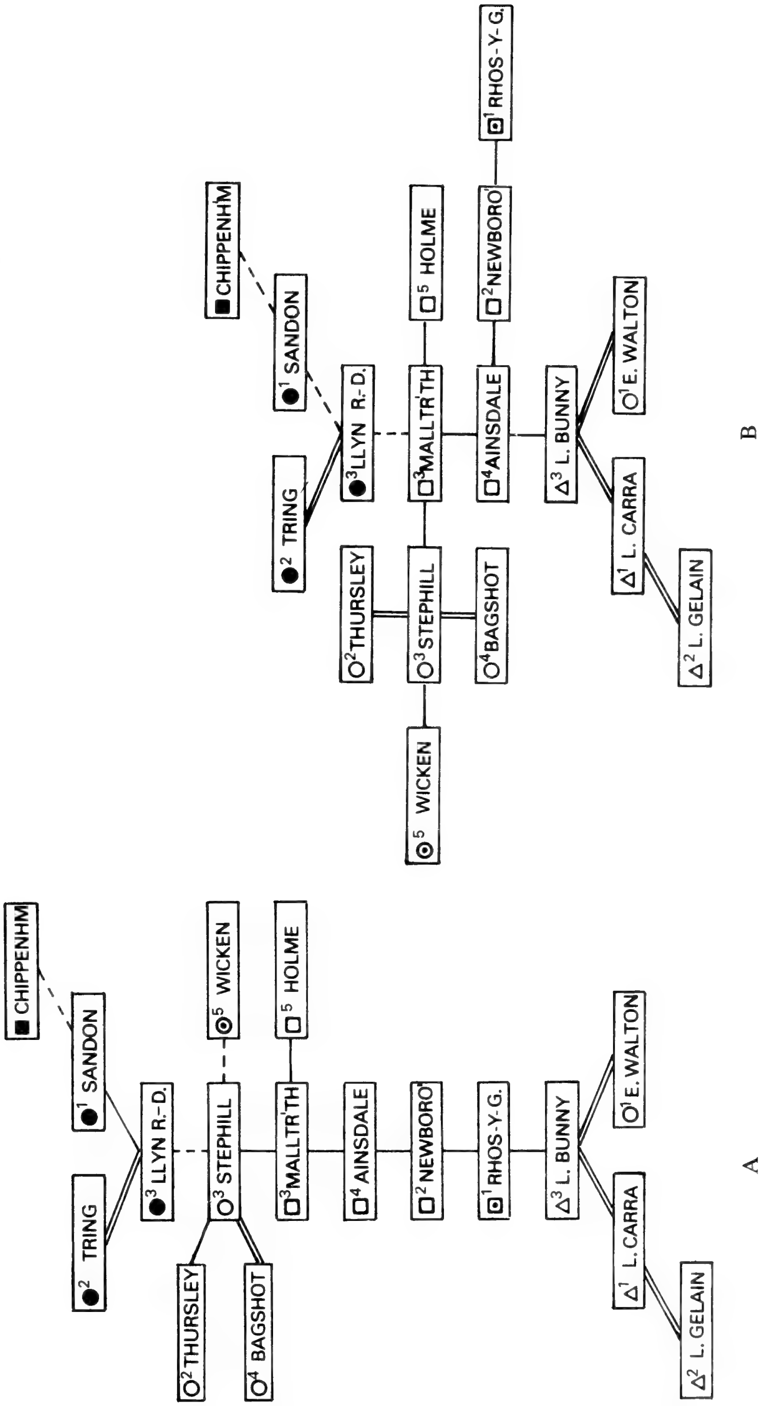


FIGURE 5. Minimum spanning trees expressing the maximum similarities of populations.
A – Based on population means for 44 characters, including floral pigmentation characters.
B – Based on population means for 36 characters, excluding floral pigmentation characters.
Double line, maximum similarity >93%; single line, 90–93%; dashed line, <90%.
See Fig. 2 for explanation of symbols.

GEOGRAPHICAL SEPARATION

The ranges of *D. incarnata* subsp. *cruenta* and subsp. *ochroleuca* are sufficiently restricted and disjunct to prevent interbreeding, but the other subspecies are distributed throughout the British Isles (Table 7) (Perring & Sell 1968). Morphological variation of *D. incarnata* is largely independent of geography, which is therefore an unlikely cause of reproductive isolation.

ECOLOGICAL SEPARATION

Heslop-Harrison (1954, 1956, 1968) emphasised the ecological component of variation between subspecies of *D. incarnata*, describing them as "habitat races" and suggesting that each is physiologically superior in its preferred habitat(s). However, the subspecies differ only in their relative ranges of habitat tolerance (Table 7). *D. incarnata* subsp. *cruenta* and subsp. *ochroleuca* are almost confined to calcareous fens, whereas subspp. *incarnata*, *coccinea* and *pulchella* grow in a wider range of habitats, where they occasionally coexist. Only populations of *D. incarnata* subsp. *pulchella* in extensive acid *Sphagnum* bogs are effectively ecologically isolated.

However, these broadly similar ecological distributions may obscure subtle differences in microecological requirements, which are most apparent where subspecies occur together. For instance, in a field near Rathkeale, Co. Limerick, *D. incarnata* subsp. *pulchella* occupied a series of depressions that were separated by ridges supporting mainly subsp. *coccinea* (Heslop-Harrison 1956). However, separation into definable microhabitats is much less pronounced in most mixed-subspecies populations of *D. incarnata*, and although the Rathkeale population apparently demonstrated some physiological differentiation, this does not explain the apparent lack of hybridization of red- and purple-flowered plants (though progeny of crosses between subspecies of different flower colours are difficult to identify without careful colour matching). We observed some microhabitat specialization of these subspecies at Rhos-y-gad, but plants that resembled *D. incarnata* subsp. *coccinea* in most characters had flowers which contained some purple anthocyanin that may have resulted from introgression with subsp. *pulchella*.

PHENOLOGICAL SEPARATION

Heslop-Harrison (1954, 1956) stated that *D. incarnata* subspp. *coccinea*, *cruenta* and *pulchella* often flower 7–14 days later than subsp. *incarnata* at similar latitudes, and suggested that this results in partial phenological isolation. We observed smaller mean differences in the flowering periods of these subspecies relative to subsp. *incarnata* (4–7 days, Table 2) that were insignificant compared to large differences in peak flowering periods of populations of the same subspecies, e.g. the four week difference in peak flowering times of morphologically similar populations of *D. incarnata* subsp. *coccinea* at Malltraeth and Holme. Moreover, the protracted flowering periods of dactylorchids means that differences in peak flowering times of coexisting taxa must be large to prevent cross-pollination.

OTHER POTENTIAL ISOLATING MECHANISMS

Their overlapping geographical and macroecological distributions allow subspecies to occur together at many sites where they may flower contemporaneously. There are several mechanisms that could prevent hybridization in such mixed-subspecies populations. Self-pollination of *D. incarnata* has been achieved artificially (Heslop-Harrison 1956), but the movement of stalks of removed pollinia to attain a suitable position for stigmatic contact is slow and makes cross-pollination more likely (Darwin 1877; Heslop-Harrison 1956). Differences between subspecies in flower colour and markings may result in pollinator specificity and provide a secondary isolating mechanism that preserves the integrity of coadapted gene complexes, though this hypothesis has not been tested in the field. Artificial crosses between several pairs of subspecies of *D. incarnata* were invariably successful (Heslop-Harrison 1956), so pollen germination and gametic fusion must have been unimpaired. Furthermore, extensive introgression of *D. fuchsii* and *D. majalis* subsp. *purpurella* (T. & T. A. Stephenson) D. Moresby Moore & Soó (Lord & Richards 1976) suggests that the more closely related subspecies of *D. incarnata* are unlikely to be separated by intrinsic barriers to either cross-pollination or the development of fertile progeny.

TABLE 7. GEOGRAPHICAL AND ECOLOGICAL DISTRIBUTIONS AND FLOWERING PERIODS OF THE SUBSPECIES OF *D. INCARNATA* IN THE BRITISH ISLES

Subspecies	Geographical distribution	Ecological distribution	pH range	Flowering periods, relative to subsp. *incarnata*
incarnata	Throughout the British Isles	Fens, marshes, dune marshes, water meadows, less frequently dune slacks	(6–)6·5–8	Late May to late June (to early July)
coccinea	Throughout the British Isles, mainly coastal	Dune slacks, less frequently dune marshes and inland meadows (especially in Ireland)	(6–)7–8	Contemporaneous (e.g. in Ireland) to 14 days later (e.g. in the Hebrides)
cruenta	W. Ireland (Co. Galway, Co Mayo, Co. Clare), also W. Scotland	*Schoenus*/*Cladium* fens, mostly at lough-sides	(7–)7·5–8+	Variable, from contemporaneous to 14 days later
pulchella	Throughout the British Isles	*Schoenus*/*Cladium* fens, *Carex*/*Phragmites* 'poor' fens, *Sphagnum* bogs.	4·5–7·5(–8)	Variable, from contemporaneous (e.g. in Ireland) to 14+ days later (e.g. in Dorset/Hampshire)
ochroleuca	East Anglia, possibly also W. Ireland and S. Wales	*Schoenus*/*Cladium*/*Phragmites* fens	(7–)7·5–8	Contemporaneous

Data from several sources and modified according to the authors' observations.

CLASSIFICATION

The classification and diagnostic descriptions that follow are based on our principal coordinates (Figs. 3 & 4, Tables 5 & 6), minimum spanning trees (Fig. 5) and population means (Table 3). Data published by Heslop-Harrison (1948, 1956) and unpublished data of N. R. Campbell (pers. comm. 1981) have also been considered.

The following terms are used to describe the frequencies of character states in taxa: rarely, less than 20% of individuals; occasionally, 20–50%; often, 51–80%; usually, greater than 80%. Frequencies of the best diagnostic characters (italicized) show most discontinuity between subspecies. Some terms used in the descriptions are qualitative but are derived from quantitative measurements:

Leaf distribution: strongly crowded towards the base, index 'h' value=0–20%; slightly crowded towards the base, h=21–40%; more-or-less evenly distributed along stem, h=41–60%.
Leaf shape: narrow, index 'g' value less than 0·15.
Density of labellum pigments: dark, reflectivity=8–20%; moderate, reflectivity=21–40%; pale, reflectivity=41–80%; very pale, reflectivity=81–89%.
Depth of labellum sinuses: deep, index 'b' value greater than 1·3.
Prominence of central labellum lobe: prominent, index 'c' value equal to or greater than 1 mm.
Reflexion of lateral labellum lobes: strongly reflexed, lobes subtend an angle of less than 40° (character states 5 or 6 in Fig. 1).
Soil pH: acid, <6; neutral, 6–7; alkaline, >7.

The taxonomy of diploid marsh-orchids is complicated by extensive synonymy (listed for all taxa) and by ambiguous original descriptions for *D. incarnata* subspp. *incarnata*, *cruenta* and *ochroleuca* (nomenclatural problems concerning these subspecies are discussed after their detailed descriptions). Several of the many varieties and forms of *D. incarnata* described by Continental workers (cf. Vermeulen (1949) and Landwehr (1977) for *D. incarnata* as a whole and Neuman (1909) for subsp. *cruenta*) occur in the British Isles, but they have been omitted from this classification because they are barely distinguishable.

Genus *Dactylorhiza* Necker ex Nevski, *Acta Inst. bot. Acad. sci. URSS*, **4**: 332 (1937).
Sect. *Maculatae* (Parlatore) Vermeulen, *Stud. Dactyl.* 65 (1947).

1. *DACTYLORHIZA INCARNATA* (L.) Soó, *Nom. nov. gen.* Dactylorhiza 3 (1962).
Orchis incarnata L., *Fl. Suecica*, 2nd. ed., 312 (1755); *O. mixta* Retzius var. *incarnata* (L.) Retzius, *Fl. Scand. Prodr.* 167 (1779); *O. latifolia* L. var. *incarnata* (L.) Cosson & Germain, *Fl. Paris*, 2nd ed., 684 (1861); *Dactylorchis incarnata* (L.) Vermeulen, *Stud. Dactyl.* 65 (1947).
Orchis impudica Crantz, *Stirpes Austriacae* 497 (1769).
Orchis divaricata Richard in Mérat, *Fl. Paris.* 345 (1812).
Orchis strictifolia Opiz, in *Naturalientausch*, **10**: 217 (1825).
Orchis angustifolia Wimmer & Grabowski, *Fl. Silesiae* 252 (1829); *O. latifolia* L. var. *angustifolia* (Wimmer & Grabowski) Babington, *Manual Br. Bot.* 291 (1843).
Orchis lanceata Dietrich, *Fl. Konigreichs* 11 (1833).
Orchis latifolia L. var. *longibracteata* Neilreich, *Fl. Wien* 129 (1846).
Orchis latifolia auct., sic Pugsley, in *Bot. J. Linn. Soc.*, **49**: 577 (1935).

Stem (8–)10–35(–45) cm, 3–9(–12) mm in diameter, often lacking anthocyanins. Basal 1f or sheath (0–)1, broadest at middle or somewhat below middle; sheathing lvs (2–)3–4(–5), ±evenly distributed along stem to strongly crowded towards the base, upright or recurved, narrowly to broadly lanceolate, usually broadest above the base, longest 1f usually also widest, 4–15 cm long, widest 1f 1–3·5 cm wide, width/length ratio of lvs decreasing up stem (often±constant in subsp. *cruenta*), yellowish-green to bright green, hooding of tips poorly- or less frequently well-developed; non-sheathing lvs (0–)1(–2), narrow, broadest at base; lvs unmarked (solid markings on both surfaces or less frequently on upper surface only in some individuals of subsp. *cruenta*). Inflorescence usually 2·5–8 cm, 15–50% of stem length, fls usually 8–40, fairly lax to dense (3–7·5 fls/cm). Basal bracts greatly exceeding ovaries (and usually flowers), floral bracts 1–2(–4) times the length of the ovaries, often suffused with anthocyanins (rarely spotted in subsp. *cruenta*); peripheral bract cells 40–70 μm long, barrel-shaped to sub-triangular. Labellum width exceeding or less frequently ± equalling length, 4·5–8×5–9 mm, usually broadest ± at middle, rarely above (obtriangular) or below (deltoid), base colour varying densities (reflectivity 8–85%) of purple-violet, purple, red-purple, red, or yellow (very rarely white); markings pale to bold dashes and/or loops (absent from subsp. *ochroleuca* and anthocyanin-less individuals of other subspecies), often covering about two-thirds of the labellum, occasionally covering most of the labellum or concentrated at its centre; sinuses present (labellum three-lobed) or less frequently absent (labellum entire), only occasionally deep (especially subsp. *ochroleuca*); central lobe equalling or exceeding lateral lobes; lateral lobes often entire, moderately to strongly reflexed; lateral outer perianth segments slightly above horizontal to near-vertical, often with solid or less frequently annular markings (absent from subsp. *ochroleuca* and anthocyanin-less individuals of other subspecies); median outer perianth segment and inner perianth segments connivent; spur slightly to moderately decurved (rarely straight), 5·5–8×2·5–5·4 mm at entrance, 2–3·5 mm halfway along (when flattened), slightly tapering, half as long to nearly as long as the ovary. $2n=40$. Flowering late May to early July (rarely later in the north). Locally frequent throughout the British Isles.

There has been considerable controversy concerning the correct specific epithet for the plant presently known as *D. incarnata*. Pugsley's (1935) detailed argument for the use of *Orchis latifolia* L. (Linnaeus 1745) prevailed in Britain, but Continental workers such as Mansfeld (1938) and Vermeulen (1947a,b) stated that *O. latifolia* should be discarded as a *nomen ambiguum*. Mansfeld advocated the use of *O. strictifolia* Opiz (Opiz 1825), but Vermeulen preferred *Orchis incarnata* L. (Linnaeus 1755), which he renamed *Dactylorchis incarnata* (L.) Vermeulen. *D. incarnata* was subsequently used by most British and Continental botanists, though *O. strictifolia* was favoured by many Scandinavian botanists and by Clapham (1952). The relative merits of *O. incarnata* and *O. latifolia* were debated in three papers published simultaneously by Vermeulen (1947b), Pugsley (1947) and Wilmott (1947). These papers contained some intriguing theories, exemplified by Wilmott's assertion that "There is no doubt that . . . the specimen representing *Orchis latifolia* in the Linnaean Herbarium . . . is *O. incarnata* auct. of the form met with when a cow-pat has been dropped upon the plant"!

The use of *O. latifolia* declined thereafter, and it was eventually declared a *nomen rejiciendum* by the 1975 Leningrad Botanical Congress. The compelling reasons for its rejection were summarized by Vermeulen (1976). However, Pugsley's (1935, 1947) arguments against *incarnata* as a specific epithet are also persuasive; the morphology intended by Linnaeus (1755) for the typification of *O. incarnata* is unclear (he apparently changed his mind at least twice). Nevertheless, we cannot recommend the rejection of *Dactylorhiza incarnata* now that it has finally gained general acceptance among European botanists.

a. Subsp. *INCARNATA*

Orchis incarnata L., *Fl. Suecica*, 2nd. ed., 312 (1755); *Dactylorchis incarnata* (L.) Vermeulen subsp. *lanceata* (Dietrich) Vermeulen, *Stud. Dactyl.* 108 (1947).
Orchis incarnata L. var. *lanceata* Reichenbach f., *Icon. Fl. Germ.* 51 (1851); *O. incarnatus* L. subsp. *lanceatus* (Reichenb. f.) Blytt & Dahl, *Handb. Norges Fl.* 227 (1906).
Orchis strictifolia Opiz subsp. *strictifolia* sensu Clapham in Clapham *et al.*, *Fl. Br. Isl.* 1318 (1952).

Stem usually >20 cm, *usually >6 mm in diameter*, usually lacking anthocyanins. Sheathing lvs usually more than 3 (occasionally 5), usually moderately to strongly crowded towards the base of the stem, longest lf usually >9 cm long, rarely narrow, *widest lf usually >2 cm wide*, lower lvs usually broadest well above the base; lf markings absent (present in f. *punctata*). *Inflorescence usually >5 cm*, usually <30% of stem length, *fls usually more than 25*. Basal bracts often >25 mm, floral bracts often <18 mm, usually less than twice the length of the ovaries, usually lacking anthocyanins. Labellum often less than 6·5×8 mm; *base colour pale, dilute red-purple or red* (i.e. pink: x=305–345, y=285–305); markings usually including several dashes, rarely bold, often concentrated in the centre of the labellum; sinuses usually shallow or absent; central lobe rarely prominent; lateral lobes usually entire, often strongly reflexed; lateral outer perianth segments usually nearer vertical than horizontal, annular markings absent; spur often <3·5 mm wide at entrance, <2·8 mm halfway along. Distributed throughout the British Isles, most frequent in England and Wales. Alkaline or neutral soils.

Our data suggest that *D. incarnata* subsp. *incarnata* is characteristically vegetatively robust (stems and leaves broad, inflorescences large), though most of the populations of subsp. *incarnata* measured by Heslop-Harrison (1956) had narrower leaves and longer spurs than our study populations. Plants at Sandon had unusually large labella, often with the normally solid pair of loop markings broken into dashes, and are thus intermediate in floral characters between *D. incarnata* subsp. *incarnata* and subsp. *gemmana* as described by Heslop-Harrison (1954, 1956).

Six of the seven plants of *D. incarnata* subsp. *incarnata* illustrated by Nelson (1976) were purple-flowered, and Landwehr (1977) also attributed several of the purple-flowered specimens he illustrated to subsp. *incarnata*. The inclusion of purple-flowered plants in *D. incarnata* subsp. *incarnata* by many Continental orchidologists reflects their apparent lack of understanding of *D. incarnata* subsp. *pulchella* (see discussion of subsp. *pulchella*).

i. f. **punctata** (Vermeulen) Bateman & Denholm, **comb. nov.**
Basionym: *Dactylorchis incarnata* (L.) Vermeulen f. *punctata* Vermeulen, *Ned. kruidk. Archf.*, **56**: 209 (1949).

Sheathing lvs with a few small dots on upper surface, usually concentrated towards the lf tips.

This form has been recorded from Coll, Outer Hebrides (Heslop-Harrison 1948) and from Malham, Yorkshire (R. H. Roberts pers. comm. 1982). Most of the other 18 varieties and forms of *D. incarnata* described by Vermeulen (1949) are referable to subsp. *incarnata* and many occur in the British Isles, but they are insufficiently distinct to justify continued recognition.

b. Subsp. *COCCINEA* (Pugsley) Soó, *Nom. nov. gen.* Dactylorhiza 4 (1962).
Orchis latifolia L. var. *coccinea* Pugsley, in *Bot. J. Linn. Soc.*, **49**: 579 (1935); *O. strictifolia* Opiz subsp. *coccinea* (Pugsley) Clapham, *Fl. Br. Isl.* 1319 (1952); *Dactylorchis incarnata* (L.) Vermeulen subsp. *coccinea* (Pugsley) Heslop-Harrison f., in *Ber. geobot. Forsch. Inst. Rübel*, **1953**: 54 (1954).
Orchis incarnata L. var. *dunensis* Druce, in *Rep. botl Soc. Exch. Club Br. Isl.*, **4**: 212 (1916); *Dactylorchis incarnata* (L.) Vermeulen var. *dunensis* (Druce) Vermeulen, in *Ned. kruidk. Archf.*, **56**: 207 (1949); *Dactylorhiza incarnata* (L.) Soó var. *dunensis* (Druce) Landwehr, in *Orchideëen*, **37**: 80 (1975).
Orchis incarnata L. f. *atriruba* Godfery, *Mon. Icon. Br. nat. Orchidaceae* 187 (1933).

Stem usually <20 cm (occasionally <10 cm), usually <6 mm in diameter, *often suffused with anthocynanins*. Sheathing lvs often more than 3, often strongly crowded towards the base of the stem, longest lf often <9 cm, occasionally narrow, widest lf usually <2 cm wide, lower lvs usually broadest well above the base; lf markings absent. Inflorescence often <5 cm, often >30% of stem length, fls usually less than 25. Basal bracts usually <25 mm, floral bracts usually <18 mm, less than twice the length of the ovaries (occasionally shorter than the ovaries), *usually suffused with anthocyanins*. Labellum usually less than 6·5×8 mm; *base colour dark or less frequently moderate, red or red-purple* (x=430–580, y=250–325); markings usually including several dashes, rarely bold, rarely concentrated in the centre of the labellum; sinuses usually shallow or absent; central lobe rarely prominent; lateral lobes often indented, usually strongly reflexed; lateral outer perianth segments usually nearer vertical than horizontal, annular markings usually absent; spur often <3·5 mm wide at entrance, <2·8 mm halfway along. Distributed throughout the British Isles, most frequent along the west coasts. Alkaline or neutral soils.

Previous literature contains several conflicting statements concerning characters that separate *D. incarnata* subsp. *coccinea* from subsp. *incarnata*; leaves of subsp. *coccinea* are said to be fewer (Wiefelspütz 1976a) and darker green (Heslop-Harrison 1948; Wiefelspütz 1976a; Lang 1980), labella are said to be smaller (Clapham 1952), less reflexed and less boldly marked (Pugsley 1935). Soó (1980) stated that *D. incarnata* subsp. *coccinea* has erect leaves, whereas most previous authors (Godfery 1933; Pugsley 1935; Heslop-Harrison 1956) had emphasised the value of its spreading, frequently recurved leaves as a diagnostic character. Although Heslop-Harrison (1948, 1954) and Sundermann (1980) stated that *D. incarnata* subsp. *coccinea* flowers two weeks later than subsp. *incarnata*, this was only observed at Holme where *D. incarnata* subsp. *coccinea* flowers especially late; subsp. *coccinea* and subsp. *incarnata* were contemporaneous at Newborough and Ainsdale.

Populations of *D. incarnata* subsp. *coccinea* growing in exposed dune slacks, e.g. Newborough and Ainsdale, tend to be shorter (*c.* 10 cm, so that the inflorescence forms a greater proportion of the length of the stem) and have leaves that are often recurved, shorter, broadest closer to their bases and more crowded towards the base of the stem than the leaves of subsp. *coccinea* growing in less exposed dune slacks (e.g. Holme) or stabilized 'dune meadows' (e.g. Malltraeth).

The population of *D. incarnata* at Rhos-y-gad is one of many variable populations of this species that occur in dune systems and inland in the north and west, and are particularly abundant on Anglesey (Summerhayes 1951; Perring & Sell 1968). Rhos-y-gad plants have the reddish-brown bract and stem anthocyanins that characterize *D. incarnata* subsp. *coccinea*, and their mean values for vegetative characters are similar to the Holme and Malltraeth populations (Table 3); they therefore occur with other individuals of *D. incarnata* subsp. *coccinea* in Fig. 4. However, they differ from the other populations of *D. incarnata* subsp. *coccinea* in a few characters; they have narrower spurs, annular outer perianth segment markings and red-purple (often described as rose-red) flowers. These presumably contain both red and violet-purple anthocyanins (see 'Variation in Single Characters'), the violet-purple component possibly being derived from *D. incarnata* subsp. *pulchella* at Rhos-y-gad, and their reflectivities range from pale to dark (Fig. 2). Consequently, they occur throughout the zone of overlap of *D. incarnata* subsp. *coccinea* with subsp. *pulchella* and subsp. *cruenta* on the principal coordinates plot that includes floral pigmentation characters (Fig. 3). Landwehr (1977) illustrated comparable Continental plants and named them *D. incarnata* f. *dunensis*, and Druce's (1916) description of its basionym, *Orchis incarnata* var. *dunensis*, also specified rose-red flower colour rather than the maroon that is more typical of *D. incarnata* subsp. *coccinea*. However, this subtle colour difference is insufficient to justify separating populations such as the one at Rhos-y-gad from subsp. *coccinea* to form an additional taxon.

c. Subsp. *CRUENTA* (O. F. Müller) P. D. Sell, in *Watsonia*, **6**: 317 (1967).

Orchis cruenta O. F. Müller, *Fl. Danica*, 15: 4, t.876 (1782); *O. latifolia* L. var. *cruenta* (O. F. Müller) Lindley, *Gen. et spec. Orchid.* 260 (1835); *O. incarnatus* L. var. *cruentus* (O. F. Müller) Blytt & Dahl, *Handb. Norges Fl.* 227 (1906); *O. incarnatus* L. subsp. *cruentus* (O. F. Müller) Ascherson & Graebner, *Synop. Mitteleurop. Fl.* 720 (1907); *Dactylorchis cruenta* (O. F. Müller) Vermeulen, *Stud. Dactyl.* 66 (1947); *D. incarnata* (L.) Vermeulen subsp. *cruenta* (O. F. Müller) Heslop-Harrison f., in *Ber. geobot. Forsch. Inst. Rübel*, **1953**: 54 (1954); *Dactylorhiza cruenta* (O. F. Müller) Soó, *Nom. nov. gen.* Dactylorhiza 4 (1962).

Orchis haematodes Reichenbach, *Fl. Germ. Excurs.* 126 (1830); *O. cruenta* O. F. Müller var. *haematodes* (Reichenbach) Neuman, in *Bot. Notiser*, **1909**: 157 (1909); *Dactylorhiza incarnata* (L.) Soó var. *haematodes* (Reichenbach) Soó, *Nom. nov. gen.* Dactylorhiza 4 (1962).

Orchis incarnata L. var. *rhombeilabia cruenta* Reichenbach f., *Icon. Fl. Germ.* 53 (1851).

Orchis matodes Reichenbach f., *Icon. Fl. Germ.* 56, t.46 (1851).

Orchis latifolia L. var. *brevifolia* Reichenbach f., *Icon. Fl. Germ.* t.51 (1851); *O. cruenta* O. F. Müller f. *brevifolia* (Reichenbach f.) Neuman, *Sveriges Fl.* 631 (1901); *O. cruenta* O. F. Müller var. *brevifolia* (Reichenbach f.) Neuman, in *Bot. Notiser*, **1909**: 157 (1909).

Orchis incarnatus L. var. *haematodes* Schulze in Ascherson & Graebner, *Synop. Mitteleurop. Fl.* 717 (1907); *Dactylorchis incarnata* (L.) Vermeulen var. *haematodes* (Schulze) Vermeulen, *Stud. Dactyl.* 117 (1947).

Orchis cruentiformis Neuman, in *Bot. Notiser*, **1909**: 243 (1909).

Orchis cruenta O. F. Müller var. *lanceolata* Neuman, in *Bot. Notiser*, **1909**: 157 (1909); *Dactylorhiza incarnata* (L.) Soó subsp. *cruenta* (O. F. Müller) P. D. Sell var. *lanceolata* (Neuman) Landwehr, in *Orchidëen*, **37**: 80 (1975).

Orchis incarnata L. var. *hyphaematodes* Neuman, in *Bot. Notiser*, **1909**: 244 (1909); *Dactylorhiza incarnata* (L.) Soó var. *hyphaematodes* (Neuman) Landwehr, in *Orchidëen*, **37**: 80 (1975).

Stem often <20 cm, usually <6 mm in diameter, *usually suffused with anthocyanins*. Sheathing lvs often 3 or less, often slightly crowded towards the base of the stem, longest lf often <9 cm long, often narrow, widest lf usually <2 cm wide, lower lvs usually broader fairly close to (but not at) the base; lf markings occasionally present on both surfaces or much less frequently on upper surface only, solid, transversely to longitudinally elongated, usually small (<2 mm in diameter), ± evenly distributed on lvs or somewhat concentrated towards the tips. Inflorescence usually <5 cm, often <30% of stem length, fls usually less than 25. Basal bracts usually <25 mm, floral bracts usually <18 mm, usually less than twice the length of the ovaries, *suffused with anthocyanins*, rarely spotted. Labellum often less than 6·5×8 mm; *base colour intense or less frequently moderate, purple-violet/purple* (x=285–325, y=165–240); *markings often loops enclosing few if any dashes*, often bold, *often covering most of the labellum*; sinuses often shallow or absent; central lobe often prominent; lateral lobes often indented, only occasionally strongly reflexed; lateral outer perianth segments often nearer horizontal than vertical, *annular markings usually present*; spur often <3·5 mm wide at entrance, <2·8 mm halfway along. Locally frequent in western central Ireland, rare in Scotland (Continental distribution: Alps, Scandinavia and U.S.S.R.). Alkaline or, less frequently, neutral soils.

D. incarnata subsp. *cruenta* was originally described from Denmark (Müller 1782) and is now known to be widespread in Scandinavia. It was later found by H. W. Pugsley in the Alps (Gsell 1935; Pugsley 1935; Senay 1937; Wilmott 1938) and by J. Heslop-Harrison in western Ireland, where it is frequent in the lough-side fens of Co. Galway and Co. Mayo and the Burren region of Co. Clare (Heslop-Harrison 1949, 1950a, 1950b, 1952, 1954, 1956; Gough & Teacher 1950; D. M. Turner Ettlinger pers. comm. 1983). Early records for *D. incarnata* subsp. *cruenta* from Britain (Goss 1899) were attributed to *D. majalis* (Reichenbach) P. F. Hunt & Summerhayes subsp. *purpurella* (T. & T. A. Stephenson) D. M. Moore & Soó by later workers (Heslop-Harrison 1950b), but a small July-flowering population of subsp. *cruenta* has since been found in Ross (Kenneth & Tennant 1984) and further discoveries in Scotland are likely. Kenneth & Tennant (1984) listed several morphological differences between Scottish and Irish plants, but comparison of their description of Scottish plants with our data from Irish plants revealed only two apparently significant differences: Scottish plants have inflorescences of similar length but fewer flowers so they are more lax, and their labella may be more reflexed. However, the Scottish population occurred in acid hillside flushes, an unusual habitat for subsp. *cruenta*.

Floral characters of Irish and Scottish *D. incarnata* subsp. *cruenta* are consistent with descriptions of Scandinavian and Alpine plants (Müller 1782; Reichenbach 1830; Reichenbach 1851; Klinge 1898; Ascherson & Graebner 1907; Neuman 1909; Camus & Camus 1929; Pugsley 1935; Gsell 1935; Senay 1937; Wilmott 1938; Vermeulen 1947a; Heslop-Harrison 1950a, 1956; Summerhayes 1951, 1968; Senghas 1968; Beisenherz 1973; Sundermann 1975, 1980; Wiefelspütz 1976a; Nelson 1976; Landwehr 1977); labella are sub-rounded or cordate, shallowly three-lobed or less frequently entire, purple or purple-violet with bold solid loop markings enclosing few if any dashes, and the lateral lobes are usually only moderately reflexed. However, the labella of most Irish plants are larger (6–7·5×6·5–9 mm) than the labella of Continental plants (usually described as *c.* 6×6 mm). Anthocyanins occur on the upper part of the stem and on the bracts (Gsell 1935; Vermeulen 1947a; Heslop-Harrison 1950b, 1956; Summerhayes 1951; Beisenherz 1973; Kenneth & Tennant 1984). Rare anthocyanin-less individuals, such as those that we observed at Lough Carra, have pale yellow flowers.

The leaf markings of *D. incarnata* subsp. *cruenta* are usually described as small, abundant, sometimes longitudinally elongated and often merging into diffuse fields. Vermeulen (1947a) argued that markings on both leaf surfaces were always present in *D. incarnata* subsp. *cruenta*, and most authors have emphasized their importance. Heslop-Harrison (1950a, 1956) stated that *D.*

incarnata subsp. *cruenta* at Lough Carra "falls well within the total range of variation encompassed by the populations placed under subsp. *pulchella*" and that "the principal distinction lies . . . in the quite unique pigmentation of the vegetative parts of some 65% of the individuals of the colony". Furthermore, "populations of *Orchis cruenta* always contain a high proportion of individuals in which the characteristic marking is present on both sides of the foliage leaves". Elsewhere, "small numbers of leaf-marked individuals appear in similar habitats among populations otherwise simply referable to subsp. *pulchella*". Heslop-Harrison apparently believed that leaf-marked individuals should predominate in populations of *D. incarnata* subsp. *cruenta*; he therefore assigned the Lough Carra population to subsp. *cruenta* and the Lough Bunny population, which contains a smaller proportion of leaf-marked individuals, to subsp. *pulchella*.

However, leaf-marked individuals did not predominate in any of our study populations (including Lough Carra) and comprised only 30% of the total number of individuals measured.[2] Similar estimates of the frequency of leaf markings in Irish populations of *D. incarnata* subsp. *cruenta* were made by Wiefelspütz (1976a) and by D. M. Turner Ettlinger (pers. comm. 1983), who noted that leaf-marked plants predominated in only one of twelve populations examined and were absent from one. The single recorded Scottish population of *D. incarnata* subsp. *cruenta* contained unmarked individuals (Kenneth & Tennant 1984), and populations of this subspecies containing only a minority of leaf-marked individuals occur in Scandinavia (Neuman 1909) and the Alps (Gsell 1943; Heidemann 1971). Furthermore, leaf markings on both surfaces were not included in the original diagnosis of *Orchis cruenta* (Müller 1782) and were ignored by subsequent workers until Klinge (1898), suggesting that plants without leaf markings were acceptable as *D. incarnata* subsp. *cruenta* ('*O. cruenta*') if they conformed to the other morphological criteria. However, Vermeulen (1947a) reached different conclusions concerning the taxonomy of leaf-marked *D. incarnata*, *viz*:

Dactylorchis incarnata (excluding var. *haematodes* (Reichenbach) Soó and var. *hyphaematodes* (Neuman) Landwehr): sheathing lvs unspotted.

D. incarnata var. *haematodes*: sheathing lvs spotted only on upper surface (spreading according to Reichenbach (1830) but erect according to Neuman (1909)).

D. incarnata var. *hyphaematodes*: sheathing lvs spotted on both surfaces, longer than one third of the stem length, erect (erect or spreading according to Neuman (1909)).

D. cruenta: sheathing lvs spotted on both surfaces, sometimes shorter than one third of the stem length, spreading (although Vermeulen argued that *cruenta* was best treated as a subspecies of *D. incarnata*, he nevertheless retained it as a full species).

23% of the Irish plants that we examined had leaves marked on both surfaces (13% also had spotted bracts), 7% had leaves marked on the upper surface only and 70% were unmarked. Their sheathing leaves were longer than one-third of the stem length and erect or suberect. Since Vermeulen (1947a) considered that *D. incarnata* subsp. *cruenta* must have spreading leaves marked on both surfaces he would not have assigned the Irish plants to this taxon. Following his classification, the unspotted plants should be assigned to *D. incarnata* (?typical variety), those spotted only on the upper surface to *D. incarnata* var. *haematodes*, and those spotted on both surfaces to *D. incarnata* var. *hyphaematodes*. However, Heslop-Harrison (1950b) compared Irish and Swedish leaf-marked populations of *D. incarnata* and concluded that both resembled *D. cruenta* var. *lanceolata* Neuman. Although the leaves of Irish and Scottish plants agree with the original description of *D. cruenta* var. *lanceolata* in size and shape, they lack the spreading posture noted by Neuman (1909) and Vermeulen (1947a).

We do not accept that there is a fundamental distinction between plants of *D. incarnata* with erect leaves and those with spreading leaves, and we recommend the inclusion of vars. *haematodes* and *hyphaematodes* in *D. incarnata* subsp. *cruenta*. We also believe that too much emphasis has been placed on the importance of leaf markings as a diagnostic character of *D. incarnata* subsp. *cruenta*, probably because this is a visually striking character. Leaf markings were infrequent in Irish populations of *D. incarnata* subsp. *cruenta* and were not correlated with variation in floral

---

[2] In Ireland *D. incarnata* subsp. *cruenta* has a prolonged flowering period from early June to mid-July. During this period the proportion of the population with leaf markings is almost constant but the mean density of vegetative anthocyanin on the leaf-marked plants increases. The heavily marked plants also show some ecological specialization, being concentrated towards the margins of large water bodies.

characters or the presence of bract and stem anthocyanins that separated subsp. *cruenta* from the other subspecies of *D. incarnata* on the principal coordinates plot (Fig. 3, Table 5).

Examination of previous literature on leaf-marked *D. incarnata* suggests an important division into a narrow-leaved group and a broad-leaved group. The narrow-leaved group has longest sheathing leaves <1·5 cm wide with index 'g' values <0·2 and comprises *D. incarnata* var. *haematodes, D. incarnata* var. *hyphaematodes, D. incarnata* subsp. *cruenta* var. *lanceolata* and var. *brevifolia* Neuman. This group occurs in Ireland and Scandinavia. The broad-leaved group (longest sheathing leaves >1·5 cm wide, index 'g' values > 0·2, leaves generally more spreading, less keeled and less hooded) comprises *D. incarnata* subsp. *cruenta* var. *subelliptica* Neuman and var. *subtriangularis* Neuman and occurs in the Alps and Scandinavia. A biometric investigation of Continental plants is needed to confirm the validity of these two apparent groups. The similarity between *D. incarnata* subsp. *cruenta* and *D. pseudocordigera* (Neuman) Soó should also be assessed.

d. Subsp. *PULCHELLA* (Druce) Soó, *Nom. nov. gen.* Dactylorhiza 4 (1962).

Orchis incarnata L. var. *pulchella* Druce, in *Rep. botl Soc. Exch. Club Br. Isl.*, **5**: 167 (1918); *O. latifolia* L. var. *pulchella* (Druce) Pugsley, in *Bot. J. Linn. Soc.*, **49**: 578 (1935); *O. strictifolia* Opiz var. *pulchella* (Druce) Clapham in Clapham *et al.*, *Fl. Br. Isl.* 1319 (1952); *Dactylorchis incarnata* (L.) Vermeulen subsp. *pulchella* (Druce) Heslop-Harrison f., in *Ber. geobot. Forsch. Inst. Rübel*, **1953**: 55 (1954).

Orchis traunsteineri Sauter var. *serotina* Haussknecht, in *Mitt. geogr. Ges. Thüringen*, **2**: 220 (1884); *O. incarnata* L. var. *serotina* (Haussknecht) Haussknecht in Schultze, M., *Orchid. Deutsch.* 19 (1894); *O. serotinus* (Haussknecht) Schwarz, *Fl. Nürnb. Erlangen* 765 (1901); *Dactylorchis incarnata* (L.) Vermeulen var. *serotina* (Haussknecht) Vermeulen, *Stud. Dactyl.* 162 (1947); *Dactylorhiza incarnata* (L.) Soó subsp. *serotina* (Haussknecht). D. M. Moore & Soó, in *Bot. J. Linn. Soc.*, **76**: 367 (1978).

Orchis angustifolia Wimmer & Grabowski var. *haussknechtii* Klinge, *Rev.* Orchis cordigera, O. angustifolia 70 (1893).

Orchis incarnata L. var. *borealis* Neuman, in *Bot. Notiser*, **1909**: 229 (1909).

Orchis incarnata L. var. *pulchriora* Druce, in *Rep. botl Soc. Exch. Club Br. Isl.*, **7**: 419 (1927).

Orchis latifolia L. var. *cambrica* Pugsley, in *Bot. J. Linn. Soc.*, **49**: 579 (1935).

Stem often >20 cm, often <6 mm in diameter, usually lacking anthocyanins. Sheathing leaves often 3 or less, usually ± evenly distributed up the stem or slightly crowded towards its base, longest leaf often >9 cm long, often narrow, widest 1f usually <2 cm wide, lower 1vs usually broadest well above the base; 1f markings absent. Inflorescence often <5 cm, often <30% of stem length, fls often less than 25. Basal bracts often <25 mm, floral bracts usually <18 mm, less than twice the length of the ovaries, *often suffused with anthocyanins*. Labellum often less than 6·5×8 mm; *base colour dark or less frequently moderate, purple or purple-violet* (x=310−330, y=175−280); markings usually including several dashes, occasionally bold, occasionally concentrated in the centre of the labellum; sinuses usually shallow or absent; central lobe occasionally prominent; lateral lobes often entire, usually strongly reflexed; lateral outer perianth segments often nearer vertical than horizontal, annular markings often absent; spur often <3·5 mm wide at entrance, <2·8 mm halfway along. Distributed throughout the British Isles. Acid to alkaline soils.

This is the least distinct subspecies of *D. incarnata*, characterized only by purple/purple-violet flowers and the presence of bract anthocyanins. Its labella have been described as entire or subentire (Summerhayes 1951; Clapham 1962; Sundermann 1980), slightly laterally reflexed (Pugsley 1935; Clapham 1962; Sundermann 1980) and relatively large, *c.* 8 mm long (Pugsley 1935; Heslop-Harrison 1950a, 1953; Clapham 1962; Sundermann 1980). However, most of the plants that we examined had shallowly three-lobed labella (though entire labella predominated at Thursley) that were strongly laterally reflexed and *c.* 6 mm long. East Walton plants had unusually tall stems and long leaves, and labella that had short central lobes and centrally-concentrated markings. They also possessed dense bract anthocyanins and moderately reflexed labella, characters that are more typical of *D. incarnata* subsp. *cruenta*. The East Walton population is consequently connected to populations of subsp. *cruenta* on the minimum spanning trees (Fig. 5).

The habitat of *D. incarnata* subsp. *pulchella* is often described simply as acid *Sphagnum* bogs. However, it also grows with other subspecies in neutral or even moderately alkaline soils. Heslop-Harrison (1956) observed a positive correlation between the stature, leaf and labellum dimensions of *D. incarnata* subsp. *pulchella* and the pH of its rhizosphere. Although our data support these correlations for all characters except leaf width, there are exceptions for each character, e.g. plants at Thursley have the smallest labella but occur in a habitat that gave only a mildly acidic pH. The overall reduction in the sizes of structures that accompany reductions in pH are small and were only evident when population means are compared.

Many populations of *D. incarnata* subsp. *pulchella* contain anthocyanin-less individuals, which are frequent in some populations, e.g. Bagshot. Although several workers (Druce 1915; Stephenson & Stephenson 1923; Nannfeldt 1944; Summerhayes 1951; Heslop-Harrison 1956) stated that the flowers of anthocyanin-less *D. incarnata* subsp. *pulchella* are white, we have seen many such plants in eight populations and they all had pale creamy yellow flowers (Bateman & Denholm 1983b). They can be confused with *D. incarnata* subsp. *ochroleuca*, especially if they occur in neutral or alkaline fens that could support subsp. *ochroleuca*. The yellow-flowered plants that we measured at Wicken had previously been referred to *D. incarnata* subsp. *ochroleuca* (Perring *et al.* 1964) but they lacked most of the diagnostic characters of subsp. *ochroleuca*, were attached to subsp. *pulchella* on the minimum spanning trees (Fig. 5), and occurred with subsp. *pulchella* on the principal coordinates plot lacking anthocyanin-dependent floral characters (Fig. 4). This evidence strongly suggests that they are anthocyanin-less *D. incarnata* subsp. *pulchella*. The purple hue typical of *D. incarnata* subsp. *pulchella* is less obvious in flowers of only moderate reflectivity, which may superficially resemble flowers of subsp. *incarnata*. The Bagshot population of *D. incarnata* subsp. *pulchella* contained approximately equal proportions of plants with dark purple, moderate purple and very pale yellow flowers; consequently, some botanists acquainted with the site believed that these were *D. incarnata* subsp. *pulchella*, subsp. *incarnata* and subsp. *ochroleuca* respectively.

Continental workers have consistently misunderstood the nature of *D. incarnata* subsp. *pulchella*. Nelson (1976) illustrated a very atypical plant with more or less flat labella of an unusual moderate reddish-purple intermediate to *D. incarnata* subsp. *pulchella* and subsp. *coccinea*. Landwehr (1977) depicted a similarly coloured plant with a very large inflorescence, and his second illustration, a line drawing, appears to be *D. majalis* subsp. *purpurella*. Landwehr named both plants *D. purpurella* var. *pulchella*, suggesting that he confused *D. incarnata* subsp. *pulchella* with *D. majalis* subsp. *purpurella* var. *pulchella* (Druce) Bateman & Denholm. Several purple-flowered *D. incarnata* illustrated by Nelson (1976) and Landwehr (1977) as subsp. *incarnata* would be assigned to subsp. *pulchella* by most British orchidologists. Surprisingly, most Continental workers also state that *D. incarnata* subsp. *pulchella* is endemic to the British Isles (Soó 1980). They assign purple-flowered *D. incarnata* without leaf markings to either subsp. *incarnata* or subsp. *serotina* (Haussknecht) D. Moresby Moore & Soó, which is said to differ from subsp. *pulchella* by its fewer-flowered inflorescence, narrower stem and fewer (3–4), narrower (1–1·5 cm) leaves (Soó 1980) that are broadest about 2 cm above their base (Wiefelspütz 1976a). However, these characters are common in *D. incarnata* subsp. *pulchella* (Table 3), indicating that Heslop-Harrison (1956) was correct to suggest that subsp. *serotina* and subsp. *pulchella* are synonymous.

e. Subsp. *OCHROLEUCA* (Wüstnei ex Boll) P. F. Hunt & Summerhayes, in *Watsonia*, **6**: 130 (1965).

Orchis incarnata L. var. *ochroleuca* Wüstnei ex Boll, in *Arch. Ver. Freunde Naturg. Mecklenb.* **14**: 307 (1860); *O. ochroleuca* (Wüstnei ex Boll) Schur, *Enum. Plant. Transsilvaniae* 641 (1866); *O. incarnatus* race *ochroleucus* (Wüstnei ex Boll) Ascherson & Graebner, *Synop. Mitteleurop. Fl.* 719 (1907); *O. latifolia* L. var. *ochroleucà* (Wüstnei ex Boll) Pugsley, in *Bot. J. Linn. Soc.*, **49**: 578 (1935); *O. strictifolia* Opiz var. *ochroleuca* (Wüstnei ex Boll) Hylander, in *Bot. Notiser*, **1942**: 228 (1942); *O. incarnata* L. subsp. *ochroleuca* (Wüstnei ex Boll) Schwarz, in *Mitt. Thuringen bot. Ges.*, **1**: 94 (1949); *Dactylorchis incarnata* (L.) Vermeulen subsp. *ochroleuca* (Wüstnei ex Boll) Heslop-Harrison f., in *Ber. geobot. Forsch. Inst. Rübel*, **1953**: 55 (1954).

O. incarnata L. var. *straminea* Reichenbach f., *Icon. Fl. Germ.* 183 (1851); *Dactylorhiza incarnata* (L.) Soó var. *straminea* (Reichenbach f.) Soó, *Nom. nov. gen.* Dactylorhiza 3 (1962).

Stem usually >20 cm, *usually >6 mm in diameter*, anthocyanins absent. Sheathing lvs often more than 3, usually ± evenly distributed along the stem, longest lf usually >9 cm long, rarely narrow, *widest lf usually >2 cm wide*, lower lvs usually broadest well above the base; lf markings absent. *Inflorescence usually >5 cm*, usually <30% of stem length, *fls usually more than 25*. Basal bracts usually >25 mm, *floral bracts usually greater than 18 mm*, often greater than twice the length of the ovary, anthocyanins absent. Labellum usually less than 6·5×8 mm; *base colour very pale, yellow* (x=c. 350, y=c. 380) deepening towards the spur entrance; markings absent; *sinuses usually deep*; central lobe prominent; *lateral lobes often deeply indented*, usually strongly reflexed; lateral outer perianth segments often nearer horizontal than vertical, unmarked; spur usually >3.5 mm wide at entrance, >2.8 mm halfway along, often straight. Possibly confined to East Anglia. Alkaline or less frequently neutral soils.

D. incarnata subsp. *ochroleuca* is characterized by a tall, broad stem, large leaves and bracts (Pugsley 1935, 1939; Heslop-Harrison 1953, 1956; Rajchel 1964; Lundqvist 1967; Nelson 1976; Davies *et al.* 1983; Bateman & Denholm 1983b). Labella are large (usually *c.* 7×9 mm in Britain), pale yellow (though darkening towards the spur entrance), and deeply three-lobed (Pugsley 1939; Nannfeldt 1944; Summerhayes 1951; Heslop-Harrison 1953, 1956; Clapham 1962; Rajchel 1964; Lundqvist 1967; Hunt & Summerhayes 1967; Nelson 1976; Bateman & Denholm 1983b), often with notched lateral lobes (Heslop-Harrison 1956; Clapham 1962; Bateman & Denholm 1983b); they resemble labella of *D. fuchsii* in shape when mounted. The Chippenham plants conformed to all these criteria (Table 3) and occurred in an alkaline fen, the typical habitat of *D. incarnata* subsp. *ochroleuca*. A larger population of *D. incarnata* subsp. *ochroleuca* that formerly occurred at Blo Norton Fen, Norfolk resembled the Chippenham plants in most characters but had on average longer, narrower leaves and longer spurs (Heslop-Harrison 1956). Some Chippenham plants had abnormally short spurs.

Authors who have identified *D. incarnata* subsp. *ochroleuca* by its flower colour alone (Perring & Sell 1968; Sundermann 1975, 1980; Soó 1980) have often confused this subspecies with yellow-flowered anthocyanin-less individuals of other subspecies, especially subsp. *pulchella* (Pugsley 1939; Lundqvist 1967; Wiefelspütz 1976b; Bateman & Denholm 1983b). This has resulted in the publication of some erroneous records, e.g. for the pale yellow-flowered plants at Wicken and Thursley (see discussion of subsp. *pulchella*). Lundqvist (1967) even argued that yellow flowers are not obligatory for *D. incarnata* subsp. *ochroleuca*, basing his argument on a population of robust *D. incarnata* near Öland, Denmark, with unmarked three-lobed labella that were either pale yellow or deep violet.

Possibly the earliest British record for *D. incarnata* subsp. *ochroleuca* was from Kidwelly, Dyfed (Stephenson & Stephenson 1923). The plants were robust and the labella were pale yellow and deeply three-lobed, but the labella were also small (*c.* 6×6 mm) and marked with a faint but discernable pattern. Recent attempts to rediscover this population have been unsuccessful (D. M. Turner Ettlinger pers. comm. 1983). The few subsequent bona fide British records for *D. incarnata* subsp. *ochroleuca* were from East Anglian fens, where it was first found in 1936 by J. E. Lousley (Lang 1980) and one or two years later by H. W. Pugsley (Pugsley 1939). The largest populations occurred in fens in the Waveney Valley, but since these are progressively drying out as the water table falls, *D. incarnata* subsp. *ochroleuca* is now endangered in Britain.

The epithet *ochroleuca* was first used by Boll (1860: 307) to describe *D. incarnata* with yellow flowers and broad but short stems found by Wüstnei (1854) in northern East Germany (Ascherson 1907). Wüstnei (1854) stated that the plants occurred in peat bogs and alder swamps with red-(?purple-)flowered *D. incarnata*, suggesting that they may have been anthocyanin-less individuals of *D. incarnata* subsp. *pulchella* (='subsp. *serotina*'). Thus the nature of the plants that provided the basis for *Orchis incarnata* var. *ochroleuca* Wüstnei ex Boll is uncertain. Some authors (e.g. Sundermann 1980) treated *D. incarnata* subsp. *ochroleuca* as a variety, but *straminea* Reichenbach (Reichenbach 1851) has precedence at this taxonomic rank, although it was unaccompanied by written or pictorial description. Moreover, the name *straminea*, which means straw-coloured, describes *D. incarnata* subsp. *ochroleuca* and other anthocyanin-less variants of *D. incarnata* equally well. *D. incarnata* var. *straminea* should therefore be considered a *nomen ambiguum*. Landwehr (1977) argued that *D. incarnata* subsp. *ochroleuca* has bright greenish-yellow flowers and is confined to eastern Europe. He assigned paler yellow-flowered plants from western Europe to *D. incarnata* f. *ochrantha* Landwehr. We doubt the validity of this distinction; Rajchel's (1964) description of Polish *D. incarnata* subsp. *ochroleuca* (stem tall, leaves and bracts large, labella three-lobed and yellow, outer perianth segments *pale* yellow) diverges considerably from Landwehr's concept of subsp. *ochroleuca* but corresponds precisely to East Anglian populations such as that at Chippenham. Landwehr's description and illustration of *D. incarnata* f. *ochrantha*, together with its type locality (Lisdoonvarna, Co. Clare), suggest that it is anthocyanin-less *D. incarnata* subsp. *incarnata* or subsp. *pulchella*.

ACKNOWLEDGMENTS

We thank J. Robertson for assistance in the field, D. M. Turner Ettlinger for information on Irish populations of *D. incarnata* subsp. *cruenta*, Belinda Denholm for typing the manuscript and G. Bateman, N. R. Campbell and R. H. Roberts for constructive comments on the text. We are grateful to the Botanical Research Fund for financial support of our fieldwork, and to botanists throughout the British Isles who drew our attention to study sites.

REFERENCES

Alvey, N. G. *et al.* (1977). *Genstat: A General Statistical Program*. Rothamsted Experimental Station, Harpenden.

Anon. (1966). *Royal Horticultural Society colour chart*. London.

Ascherson, P. (1907). Wer ist der Autor von *Orchis incarnata* var. *ochroleuca? Arch. Ver. Freunde Naturg. Mecklenb.*, **61**: 123–125.

Ascherson, P. & Graebner, P. (1907). *Orchis; Latifolii*, in *Synopsis der mitteleuropäischen Flora* **3**: 714–755. Leipzig.

Bateman, R. M. & Denholm, I. (1983a). A reappraisal of the British and Irish dactylorchids, 1. The tetraploid marsh-orchids. *Watsonia*, **14**: 347–376.

Bateman, R. M. & Denholm, I. (1983b). *Dactylorhiza incarnata* (L.) Soó subsp. *ochroleuca* (Boll) P. F. Hunt & Summerhayes. *Watsonia*, **14**: 410–411.

Beisenherz, W. (1973). Zur Verbreitung von *Dactylorhiza cruenta* und *D. pseudocordigera* in Skandinavien. *Orchidee*, **24**: 119–120.

Blackith, R. E. & Reyment, R. A. (1971). *Multivariate morphometrics*. London.

Boll, E. (1860). Flora von Mecklenburg. *Arch. Ver. Freunde Naturg. Mecklenb.*, **14**: 1–404.

Camus, E. G. & Camus, A. (1929). Sub-gen. *Dactylorchis*, in *Iconographie des Orchidées d'Europe et du Bassin Méditerranéen*. pp. 208–243. Paris.

Clapham, A. R. (1952). *Orchis* L., in Clapham, A. R., Tutin, T. G. & Warburg, E. F. *Flora of the British Isles*, pp. 1310–1323. Cambridge.

Clapham, A. R. (1962). *Dactylorchis* (Klinge) Vermeul., in Clapham, A. R., Tutin, T. G. & Warburg, E. F. *Flora of the British Isles*, 2nd ed., pp. 1042–1049. Cambridge.

Clarke, C. B. (1882). On a Hampshire *Orchis* not represented in 'English Botany'. *Bot. J. Linn. Soc.*, **19**: 206–208.

Clausen, J., Keck, D. D. & Hiesey, W. M. (1940). Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. *Publs Carnegie Inst. Wash.*, **520**.

Cook, C. D. K. (1968). Phenotypic plasticity with particular reference to three amphibious plant species, in Heywood, V. H., ed. *Modern methods in plant taxonomy*, pp. 97–111. London.

Darwin, C. (1877). *The various contrivances by which orchids are fertilized by insects*. London.

Davies, P., Davies, J. & Huxley, A. (1983). *Wild orchids of Britain and Europe*. London.

Druce, G. C. (1915). Plant records. *Report Winchester College Natural History Society* for 1913–1915, pp. 9–13.

Druce, G. C. (1916). Notes on *Orchis*. *Rep. botl Soc. Exch. Club Br. Isl.*, **4**: 211–214.

Godfery, M. J. (1933). *Monograph and iconograph of native British Orchidaceae*. Cambridge.

Goss, H. (1899). *Orchis cruenta* in Cumberland. *J. Bot., Lond.*, **37**: 37.

Gough, K. & Teacher, D. (1950). The distribution of *Orchis cruenta* Müller. *Ir. Nat. J.*, **10**: 81–82.

Gower, J. C. (1966). Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika*, **52**: 325–338.

Gower, J. C. (1971). A general coefficient of similarity and some of its properties. *Biometrics*, **27**: 857–872.

Gower, J. C. & Ross, G. J. S. (1969). Minimum spanning trees and single linkage cluster analysis. *J. R. statist. Soc. C.*, **18**: 54–64.

Gsell, R. (1935). Über bündnerische Orchideen. *Jber. naturf. Ges. Graubündens*, **74**: 3–32.

Gsell, R. (1943). Über die Verbreitung einiger Orchideen in Graübunden. *Jber. naturf. Ges. Graübundens*, **78**: 3–46.

Heidemann, H. (1971). Eine wenig bekannte Form von *Dactylorhiza cruenta* (O. F. Müll.) Soó in den Alpen. *Orchidee*, **22**: 259–260.

Heslop-Harrison, J. (1948). Field studies in *Orchis* L., I. The structure of dactylorchid populations on certain islands in the Inner and Outer Hebrides. *Trans. Proc. bot. Soc. Edinb.*, **35**: 26–66.

Heslop-Harrison, J. (1949). *Orchis cruenta* Müll; a new Irish marsh orchid. *Ir. Nat. J.*, **9**: 329–330.

Heslop-Harrison, J. (1950a). Notes on some Irish Dactylorchids. *Ir. Nat. J.*, **10**: 82–83.

Heslop-Harrison, J. (1950b). *Orchis cruenta* Müll. in the British Islands. *Watsonia*, **1**: 366–375.

Heslop-Harrison, J. (1952). Notes on the distribution of the Irish Dactylorchids. *Veröff. geobot. Inst. Rübel, Zürich*, **25**: 100–113.

Heslop-Harrison, J. (1953). Some problems of variation in the British dactylorchids. *S. East Nat.*, **58**: 14–25.

Heslop-Harrison, J. (1954). A synopsis of the dactylorchids of the British Isles. *Ber. geobot. Forsch. Inst. Rübel*, **1953**: 53–82.

Heslop-Harrison, J. (1956). Some observations on *Dactylorchis incarnata* (L.) Vermln. in the British Isles. *Proc. Linn. Soc. Lond.*, **166**: 51–82.

Heslop-Harrison, J. (1968). Genetic system and ecological habit as factors in dactylorchid variation. *Jber. naturw. Ver. Wuppertal*, **21–22**: 20–27.

Hunt, P. F. & Summerhayes, V. S. (1965). *Dactylorhiza* Nevski, the correct generic name of the dactylorchids. *Watsonia*, **6**: 128–133.

Hunt, P. F. & Summerhayes, V. S. (1967). The genus *Dactylorhiza* in Britain. *Proc. bot. Soc. Br. Isl.*, **6**: 372–375.

Jones, S. B. Jnr & Luchsinger, A. E. (1979). *Plant systematics*. London.

Kenneth, A. G. & Tennant, D. J. (1984). *Dactylorhiza incarnata* (L.) Soó subsp. *cruenta* (O. F. Mueller) P. D. Sell in Scotland. *Watsonia*, **15**: 11–14.

Klinge, J. (1898). Dactylorchidis, Orchidis subgeneris, monographiae prodromus. *Acta Hort. Petropol.*, **17**: 145–202.

Landwehr, J. (1977). *Wilde orchideeën van Europa*. Amsterdam.

Lang, D. (1980). *Orchids of Britain*. Oxford.

Linnaeus, C. (1745). *Flora Suecica*. Stockholm.

Linnaeus, C. (1755). *Flora Suecica*, 2nd ed. Stockholm.

Lord, R. M. & Richards, A. J. (1977). A hybrid swarm between the diploid *Dactylorhiza fuchsii* (Druce) Soó and the tetraploid *D. purpurella* (T. & T. A. Steph.) Soó in Durham. *Watsonia*, **11**: 205–210.

Lundqvist, A. (1967). Orchideen Ölands. *Svensk Bot. Tidskr.*, **61**: 463–493.

Mansfeld, R. (1938). Zur Nomenklatur der europäischen Orchideengattungen. *Reprium nov. Spec. Regni veg.* **44**: 145–154.

Müller, O. F. (1782). t. 876 in Oeder, F. C. *Flora Danica* **5**. Hanover.

Nannfeldt, J. A. (1944). *Orchis strictifolia* Opiz var *ochroleuca* (Boll) Hyl., en förbisedd svensk kalkkärrväxt. *Svedburg*, **1944**: 601–622.

Nelson, E. (1976). *Monographie und Ikonographie der Orchidaceen-Gattung, III.* Dactylorhiza. Zürich.

Neuman, L. M. (1909). Anteckningar rörande nordiska Orkis-former. *Bot. Notiser.*, **1909**: 151–159, 229–246.

Opiz, P. M. (1825). *Naturalientausch* **10**, p. 217. Prague.

Perring, F. H., Sell, P. D., Walters, S. M. & Whitehouse, H. L. K. (1964). *A Flora of Cambridgeshire*. Cambridge.

Perring, F. H. & Sell, P. D., eds. (1968). *Critical Supplement to the Atlas of the British Flora*, pp. 141–143. London.

Pugsley, H. W. (1935). On some marsh orchids. *Bot. J. Linn. Soc.*, **49**: 553–592.

Pugsley, H. W. (1939). Recent work on dactylorchids. *J. Bot., Lond.*, **77**: 50–56.

Pugsley, H. W. (1947). *Orchis latifolia* L. or *O. incarnata* L.? *Rep. botl Soc. Exch. Club Br. Isl.*, **12**: 86–88.

Rajchel, R. (1964). *Orchis incarnata* L. subsp. *ochroleuca* (Wüstnei) O. Schwarz in Poland. *Fragm. flor. geobot.*, **10**: 193–197.

Reichenbach, H. G. (1851). Orchideae, in *Icones Florae Germanicae et Helveticae* **13/14**. Leipzig.

Reichenbach, H. G. L. (1830). *Orchis* L., in *Flora Germanica Excursoria*, pp. 125–127. Leipzig.

Senay, P. (1937). *Orchis cruenta* Müller, nouveau pour la flore francaise. *Bull. Soc. bot. Fr.*, **84**: 511–515.

Senghas, K. (1968). Taxonomische Ubersicht der Gattung *Dactylorhiza* Necker ex Nevski. *Jber. naturw. Ver. Wuppertal*, **21–22**: 32–67.

Sneath, P. H. A. & Sokal, R. R. (1973). *Introduction to numerical taxonomy*. San Francisco.

Soó, R. (1962). *Nomina nova generis* Dactylorhiza. Budapest.

Soó, R. (1980). *Dactylorhiza* Necker ex Nevski, in Tutin, T. G. *et al.*, eds. *Flora Europaea*, **5**: 333–337. Cambridge.

Stace, C. A. (1975). *Hybridization and the flora of the British Isles*, pp. 1–90. London.

Stephenson, T. & Stephenson, T. A. (1923). The British forms of *Orchis incarnata*. *J. Bot., Lond.*, **61**: 273–278.

SUMMERHAYES, V. S. (1951). *Wild orchids of Britain*. London.

SUMMERHAYES, V. S. (1968). *Wild orchids of Britain*, 2nd ed. London.

SUNDERMANN, H. (1975). *Europäische und mediterrane Orchideen – Eine Bestimmungsflora*, 2nd ed. Hildesheim.

SUNDERMANN, H. (1980). *Europäische und mediterrane Orchideen – Eine Bestimmungsflora*, 3rd ed. Hildesheim.

UPHOFF, W. (1979). Anthocyanins in the flowers of European orchids. *Experientia*, **35**: 1013–1014.

UPHOFF, W. (1982). Identification of European orchids by determination of the anthocyanin concentration during development of the blossoms. *Experientia*, **38**: 778–780.

VERMEULEN, P. (1947a). *Studies on dactylorchids*. Utrecht.

VERMEULEN, P. (1947b). *Orchis latifolia* L. or *O. incarnata* L.? *Rep. botl Soc. Exch. Club Br. Isl.*, **12**: 82–86.

VERMEULEN, P. (1949). Varieties and forms of Dutch orchids. *Ned. kruidk. Archf.*, **56**: 204–242.

VERMEULEN, P. (1976). Was ist *Orchis latifolia* L.? *Acta. bot. neerl.*, **25**: 371–379.

WIEFELSPÜTZ, W. (1976a). Über einige *Dactylorhiza*-Sippen in Grössbritannien und Irland. *Jber. naturw. ver. Wuppertal*. **29**: 41–51.

WIEFELSPÜTZ, W. (1976b). *Dactylorhiza incarnata* ssp. *ochroleuca* (Boll) Hunt & Summerh. auf Gotland? *Jber. naturw. ver. Wuppertal* **29**: 103–105.

WILMOTT, A. J. (1938). Un *Orchis* nouveau pour la flore de France. *Bull. mens. Soc. linn. Lyon*, **7**: 84–86.

WILMOTT, A. J. (1947). *Orchis latifolia* L. or *O. incarnata* L.? *Rep. botl Soc. Exch. Club Br. Isl.*, **12**: 88–92.

WÜSTNEI, K. (1854). pp. 95–96, in KOCH, F., Bericht über die am 9 Juni unternommene Excursion nach der Umgegend von Sternberg. *Arch. Ver. Freunde Natur. Mecklenb.*, **8**: 92–97.

(*Accepted December 1984*)

Peloria and pseudopeloria in British orchids

R. M. BATEMAN

Geology Department, Chelsea College (London University), 552 Kings Road, London, SW10 0UA

ABSTRACT

Peloric orchids have either (a) the lateral, inner perianth segments replaced by additional labella or (b) the labellum replaced by a third, undifferentiated, inner perianth segment. Type (a) mutants have been reported for several British and Irish orchid species, but type (b) mutants are extremely rare. Aberrant orchids with poorly differentiated labella that resemble their outer perianth segments ('sepaloid') are best described as pseudopeloric. They have often been misidentified as type (b) peloric individuals or as hybrids, and are more frequent than has previously been suggested.

PELORIA

All our native orchid species normally have zygomorphic (bilaterally symmetrical) flowers. However, rare mutants have actinomorphic (radially symmetrical) perianth segments, although the column remains bilaterally symmetrical; actinomorphic mutants of normally zygomorphic flowers are termed peloric. Peloria in orchids occurs when (a) the inner perianth segments are replaced by two additional labella (and spurs if these are normally present in the species), or (b) the labellum is replaced by a third, undifferentiated, inner perianth segment. Type (a) mutants have been reported for *Cephalanthera damasonium* (Mill.) Druce (C. B. Tahourdin, unpublished circular 1926), *Corallorhiza trifida* Chatel. (Webster 1967; Rodway 1972), *Listera ovata* (L.) R. Br. (Summerhayes 1951), *Ophrys insectifera* L. (Tahourdin 1925; Godfery 1933; Webster 1967; Lang 1980; D. M. Turner Ettlinger pers. comm. 1983), *O. apifera* Huds. (Godfery 1933; Webster 1967), *O. fuciflora* (F. W. Schmidt) Moench (Godfery 1933), *Orchis morio* L. (Tahourdin 1925; Godfery 1933), *O. purpurea* Huds. (Godfery 1933; Rose 1949; Lang 1980; D. M. Turner Ettlinger pers. comm. 1983), *Anacamptis pyramidalis* (L.) L. C. M. Richard (Godfery 1933), and *Gymnadenia conopsea* (L.) R. Br. (I found a single plant on Ivinghoe Beacon, Bucks., v.c.24, in 1982). Genuine type (b) mutant orchids appear to be unrecorded in Britain, although rare individuals with this floral configuration have been found in Europe; e.g. *Orchis purpurea* in France (Godfery 1933) and *Ophrys tenthredinifera* Willd. in Mallorca (J. Robertson pers. comm. 1984).

PSEUDOPELORIA

In a third group of rare mutants the labellum is poorly differentiated and is similar to, but not identical with, the outer perianth segments. These labella are often described as 'sepaloid', and flowers possessing such labella as 'semi-peloric'. However, this term is inappropriate as orchid flowers are either bilaterally or radially symmetrical, i.e. non-peloric or peloric; 'pseudopeloric' is a more apt description. The classic example is the mutant variant of *Ophrys apifera*, illustrated by Tahourdin (1925), Godfery (1933), Summerhayes (1951) and Lang (1980), that has an unusual unmarked labellum similar in colour, size and overall shape to the outer perianth segments. However, the labellum differs from the outer perianth segments in possessing lateral indentations that may represent traces of the deep sinuses which divide normal labella into three lobes.

Reports of possible pseudopeloria in *O. fuciflora* (Smith 1852) and *Epipactis helleborine* (L.) Crantz (Young 1952a) are poorly documented, and the most widespread example of pseudopeloria in British orchids has not previously been recognized as such: *Epipactis phyllanthes* G. E. Smith var. *phyllanthes* has a labellum that lacks the constriction which separates the epichile and

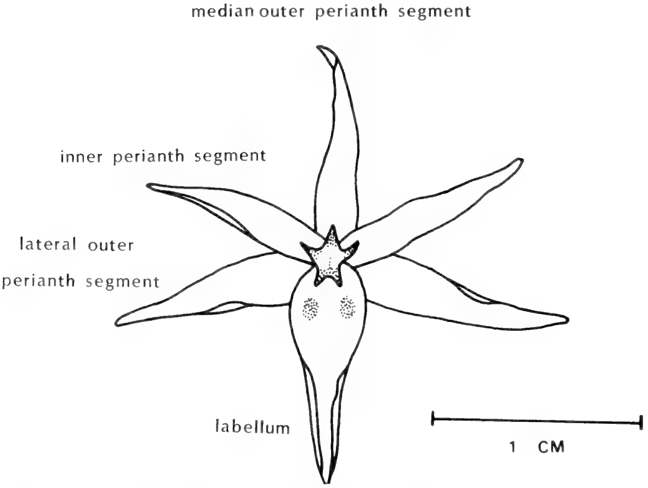


FIGURE 1. Aberrant *Dactylorhiza fuchsii* from Pitstone Fen, Bucks.

hypochile of other *Epipactis* and consequently resembles the outer perianth segments, i.e. it is 'sepaloid' (Young 1952a,b) and the flowers are therefore pseudopeloric.

Lang (1980) illustrated a *Gymnadenia conopsea* flower with three identical outer perianth segments that are abnormally straight, broad and acute. The inner perianth segments and labellum are replaced by three spurless structures that resemble the outer perianth segments but possess two basal protruberances that probably represent traces of the lateral lobes of normal labella. This plant appears to show both type (a) peloria and pseudopeloria; pseudopeloria is not partial peloria, as was suggested by its previous description 'semi-peloria', but is a separate and distinct phenomenon.

In 1982, R. Simms discovered two unusually late-flowering and lax specimens of *Dactylorhiza fuchsii* (Druce) Soó in an eastern Buckinghamshire fen (G. M. Atkins pers. comm. 1982) that I subsequently identified as pseudopeloric (Fig. 1). The labellum resembles that of pseudopeloric *Ophrys apifera*, being reduced to a single, slightly-deflexed, long-acuminate lobe but differentiated from the other perianth segments by a shallow distal constriction. However, unlike *O. apifera*, the other perianth segments are also abnormal, particularly the inner perianth segments which are straight, acute and approximately equal to the outer perianth segments in length. The spur is barely detectable, and the column is sterile and deformed into five almost equal lobes. The flower colour is cream tinged with pink, and the only markings are two crimson spots near the base of the labellum. The overall morphology of the flowers suggests partial regression to the putative ancestors of the orchid family, which are believed to have possessed radially symmetrical lily-like flowers (Dressler 1981; Dahlgren & Clifford 1982). Such plants appear to be very rare, as I have been unable to find any reports of similar aberrant individuals of *Dactylorhiza* in the extensive literature on this genus.

PSEUDOPELORIA AND × *PSEUDANTHERA*

Significantly, the six perianth segments of the pseudopeloric *D. fuchsii* resemble those of the supposed intergeneric hybrid × *Pseudanthera breadalbanensis* McKean (*Platanthera chlorantha* × *Pseudorchis albida*) in Perthshire, described by McKean (1982); this plant may therefore be a pseudopeloric variant of *P. chlorantha*. This interpretation is supported by four additional observations: (i) Landwehr (1977) illustrated a morphologically similar flower and described it as a mutant form of *P. chlorantha*. (ii) Most characters of the Perthshire plants are much closer to *P. chlorantha* than to *P. albida*. (iii) In 1983 the supposed hybrids occurred with two other mutant variants of *P. chlorantha*. The first mutant, which bore completely green flowers with brown pollinia, closely resembled *P. algeriensis* Batt. & Trabut (Davies *et al.* 1983: plate 60). Each flower of the second mutant possessed three spurs and a reduced labellum, showing as much morphological divergence from normal *P. chlorantha* as the supposed hybrids. (iv) Similar pseudopeloric individuals have been reported for *P. bifolia* (L.) L. C. M. Richard. A plate in Tahourdin (1925) shows flowers with 'sepaloid' labella and only a trace of a spur, and an apparently pseudopeloric individual of *P. bifolia* was found 25 km south-west of the Scottish locality for × *Pseudanthera* (Smith 1852).

CAUSE OF PSEUDOPELORIA

The cause of pseudopeloria remains speculative. Plants of *Epipactis phyllanthes* var. *phyllanthes* are not usually associated with those of other more florally-differentiated varieties of *E. phyllanthes*, probably because this species is autogamous so a pseudopeloric founder can generate a large population of similar individuals. Pseudopeloria appears to be an inherited trait. Young (1952b) suggested that 'sepaloid' labella arose in *Epipactis phyllanthes* var. *phyllanthes* either (i) by gradual loss of gene(s) determining labellum shape, or (ii) by the sudden deactivation of these genes, e.g. due to a change in a regulator gene. The absence of morphological intermediates between the pseudopeloric individuals of *Ophrys*, *Platanthera* and *Dactylorhiza* species described in this paper and plants of these species with normal flowers suggests that, for these genera at least, the second hypothesis is more plausible.

ACKNOWLEDGMENTS

I thank G. M. Atkins, J. Robertson and D. M. Turner Ettlinger for information on occurrences of peloric and pseudopeloric orchids, I. Denholm for helpful discussion, and J. M. Lund for typing the manuscript.

REFERENCES

Dahlgren, R. M. T. & Clifford, H. T. (1982). *The monocotyledons: a comparative study.* London.

Davies, P., Davies, J. & Huxley, A. (1983). *Wild orchids of Britain and Europe.* London.

Dressler, R. L. (1981). *The orchids – natural history and classification.* Cambridge, Mass.

Godfery, M. J. (1933). *Monograph and iconograph of native British Orchidaceae.* Cambridge.

Landwehr, J. (1977). *Wilde orchideeën van Europa.* Amsterdam.

Lang, D. C. (1980). *Orchids of Britain.* Oxford.

McKean, D. R. (1982). × *Pseudanthera breadalbanensis* McKean: a new intergeneric hybrid from Scotland. *Watsonia*, **14**: 129–131.

Rodway, G. (1972). Rediscovery of the coral-root orchid (*Corallorhiza trifida* Chatel.) in Ayrshire, and a peloric form. *Trans. Proc. bot. Soc. Edinb.*, **41**: 552–554.

Rose, F. (1949). *Orchis purpurea* Huds. *J. Ecol.*, **36**: 366–377.

Smith, G. E. (1852). *Epipactis phyllanthes. Gard. Chron.*, **34**: 660.

Summerhayes, V. S. (1951). *Wild orchids of Britain.* London.

Tahourdin, C. B. (1925). *Native orchids of Britain.* Croydon.

Webster, M. McC. (1967). New county records from Moray: a peloric form of *Corallorhiza trifida. Proc. bot. Soc. Br. Isl.*, **7**: 91.

Young, D. P. (1952a). Studies in the British *Epipactis*, III. *Epipactis phyllanthes* G. E. Sm., an overlooked species. *Watsonia*, **2**: 253–259.

Young, D. P. (1952b). Studies in the British *Epipactis*, IV. A revision of the *phyllanthes-vectensis-pendula* group. *Watsonia*, **2**: 259–276.

(*Accepted June 1984*)

Watsonia, **15**, 361–380 (1985)

The *Rubus* flora of Norfolk and Suffolk

A. L. BULL

Hillcrest, East Tuddenham, Dereham, Norfolk, NR20 3JJ

ABSTRACT

The distribution of species of *Rubus* recorded in Norfolk and Suffolk is given. Maps of the distributions are given for all species recorded in five or more 5 km squares.

INTRODUCTION

The *Flora of Norfolk* (Petch & Swann 1968) includes a list of brambles which, with few exceptions, was compiled by the Rev. E. F. Linton 80 years previously. It was decided to try and refind these, and a start was made in 1970 with the aid of *Rubi of Great Britain and Ireland* (Watson 1958). This proved remarkably unsuccessful. However, in 1971, E. S. Edees walked through a local wood with the author and pointed out 14 species of *Rubi* and these provided a basis on which to build. As possibility became reality, the scope of the survey extended to include the whole area bounded by the Fens and the River Stour, the two being linked by a line following the Devil's Dyke west of Newmarket, and continuing to the headwaters of the Stour near Haverhill. This was the frontier held many centuries ago by the East Angles. The area covered thus includes the whole of E. Suffolk (v.c.25), W. Suffolk (v.c.26), E. Norfolk (v.c.27), W. Norfolk (v.c.28), and a very small part of Cambridgeshire (v.c.29) east of the Devil's Dyke.

Between 1973 and 1983, one or two weeks holiday were devoted to brambles each July, as well as many other days. Concentrations of species in particular areas proved intriguing, and led to the mapping being switched from the planned recording in 10 km squares to recording within 5 km squares. In all, about 600 sites have been visited, and a full list of these has been lodged in the data banks at Norwich and Ipswich, together with a voucher collection of specimens which will be updated if other species come to light in the future.

Excluding *Rubus idaeus*, distributions have been mapped for all species which have records in five or more 5 km squares (see Figs. 1–38). Unlocalized records sent in by other observers, have been shown by a single crossed dot centrally placed in a 10 km square. Where a record lies in a 5 km square divided by a vice-county boundary, a pointer has been attached to the dot to indicate in which vice-county the record occurs. Where no pointer is present, the species occurs in both vice-counties. All the 5 km squares visited by the author, in which at least one species was recorded, are shown in Fig. 21. Records for some of the other squares have been received from other sources.

Visits were made to the following herbaria: **NWH**, **IPS**, **CGE** and **BM**. The 'Linton collection' is at the first named. This consists of sheets sent to Linton through the Botanical Exchange Club, and mostly emanating from the Rev. Augustin Ley in Hereford. Linton's own gatherings are scattered through the national herbaria (A. Newton pers. comm.). Most of W. M. Hind's voucher collections are still present in **IPS**, though these are relatively unexciting. Work done on several visits to **CGE** was particularly helpful when searching for material of certain species. This was especially true of specimens collected by the late B. A. Miles, the study of which provided much useful information. A single visit was paid to **BM**, in company with J. Ironside-Wood, who very kindly went through his collection with the author, at a time when the status of *R. norvicensis* was being critically examined.

It was soon discovered that it was not always certain which plant was actually referred to by some of the names used during the 19th century. This has meant that some detective work has been necessary to equate some of the plants found with names in the *Flora of Norfolk*. The plant listed as *Rubus rosaceus* Weihe was probably *R. hylocharis* W. C. R. Wats., formerly called *R. rosaceus* var. *sylvestris*. *Rubus fuscus* Weihe may well have been the plant recently named as *Rubus norvicensis* (Bull & Edees 1983) as the latter is abundant where Linton found the former. Similarly, the plant known for a century as *Rubus menkei* Weihe, was seen by A. Newton and Prof. H. E. Weber in 1976, and promptly renamed *Rubus iceniensis* (Newton & Weber 1977), a local endemic confined to Norfolk.

The survey has resulted in three new names so far: *Rubus iceniensis*, *R. norvicensis*, a regional endemic with a discontinuous distribution in Norfolk, Suffolk and N. Essex (v.c.19), and *R. boudiccae* (Bull & Edees 1980) another regional endemic, widespread and often abundant in Norfolk and Suffolk, and extending into Essex (v.cc. 18 and 19) at least as far as Danbury Common.

Rediscovering the brambles of more recent workers has also had its problems. H. J. Riddelsdell visited Norfolk in 1925 and recorded "*Rubus plicatus* Weihe & Nees abundant on Hargham Heath, flowers often pink". The area is now largely afforested with the brambles confined to the roadside. Among these, *R. plicatus* has not been found, but *R. arrheniiformis* W. C. R. Wats. has, and this is always pink. Moreover, Watson did not name it until eleven years after Riddelsdell's visit.

CHECK-LIST OF *RUBUS* SPECIES IN THE STUDY AREA

RUBUS IDAEUS L.
Widespread native. Especially in damp woods and carr, and on damp commons. Often supplemented by garden escapes near habitations. Amber-fruited bushes have been met with at Hopton Point, Little Cressingham, W. Norfolk (52/8.9.) and at Redgrave Fen, Suffolk (62/0.7.). Occurs in all v.cc. in the study area.

**RUBUS SPECTABILIS* PURSH
Non-critical alien, native of North America. E. Suffolk, Stall's Valley, Freston (62/1.3.) (*F. W. Simpson*).

RUBUS CAESIUS L.
Widespread in a variety of habitats, especially woods on clay. Edees (1974) considers that it flourishes on soils where *R. ulmifolius* is most frequent. Probably under-recorded, as caution has been exercised in areas where '*caesian* hybrids' were especially abundant. Occurs in all v.cc. in the study area. (Fig. 1).

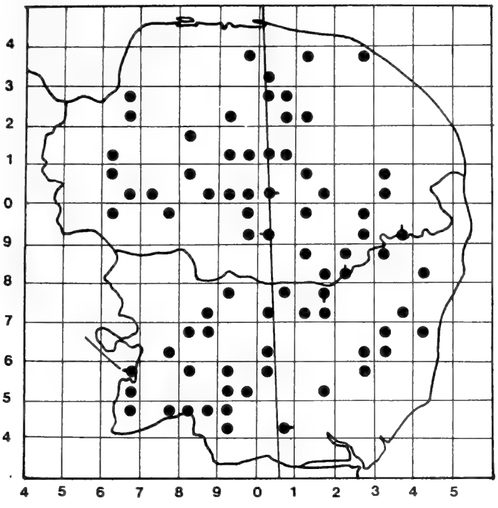
SECTION *SUBERECTI* P. J. MUELL.

RUBUS NESSENSIS W. HALL
Occurs in old woods and on undisturbed commons, its presence indicating the antiquity of the vegetation of the site. E. and W. Norfolk only. Especially fine in Swanton Novers Little Wood (63/0.3.), the upright stems often reaching 3 m or more. 62 v.cc. in England, Scotland and Wales. Ireland. Widespread in north-western Europe. (Fig. 2).

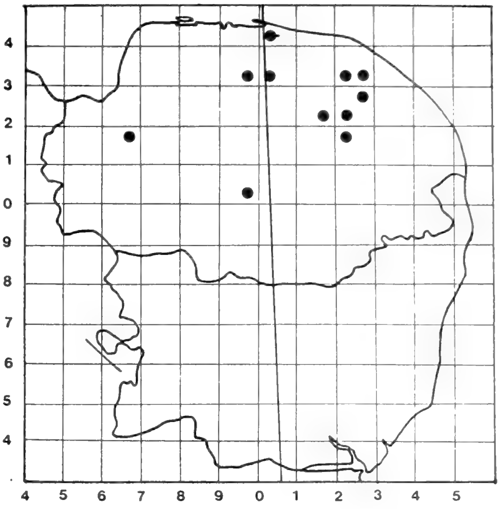
**RUBUS PERGRATUS* BLANCHARD
This North American species is a close ally of the above. E. Norfolk, Common Plantation, Aylmerton (63/1.3.). Also naturalized in Surrey, S. Essex, N. Lincs., Cheshire and Leics.

*denotes an alien species.

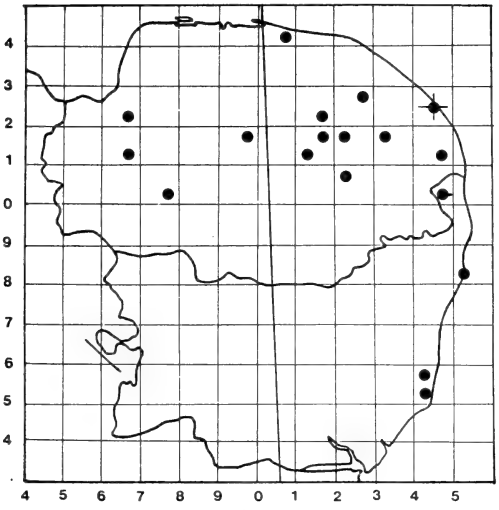
FIGURE 1. Distribution of *Rubus caesius* L.
FIGURE 2. Distribution of *Rubus nessensis* W. Hall
FIGURE 3. Distribution of *Rubus plicatus* Weihe & Nees
FIGURE 4. Distribution of *Rubus vigorosus* P. J. Muell. & Wirtg.
FIGURE 5. Distribution of *Rubus conjungens* (Bab.) Rogers
FIGURE 6. Distribution of *Rubus eboracensis* W. C. R. Wats.


4
3
2
1
0
9
8
7
6
5
4
4 5 6 7 8 9 0 1 2 3 4 5

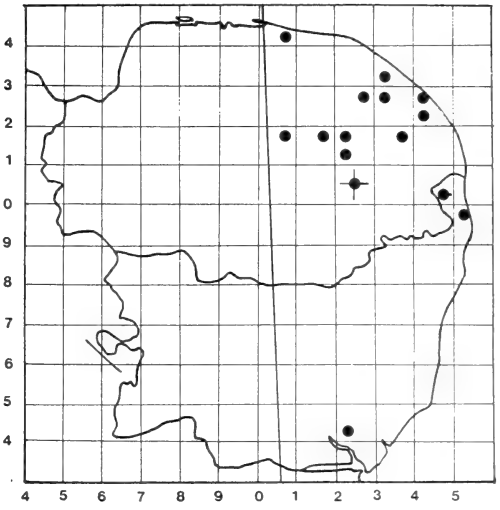
1


4
3
2
1
0
9
8
7
6
5
4
4 5 6 7 8 9 0 1 2 3 4 5

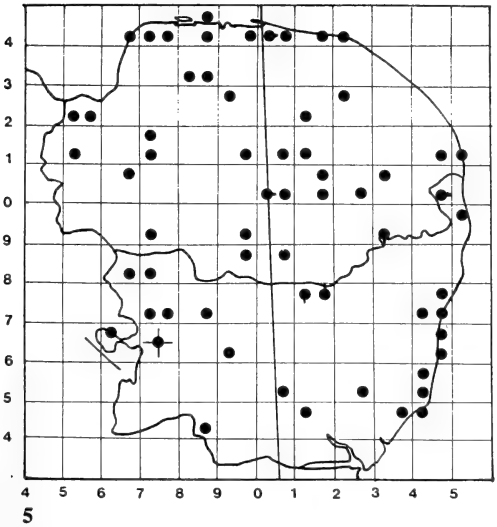
2


4
3
2
1
0
9
8
7
6
5
4
4 5 6 7 8 9 0 1 2 3 4 5

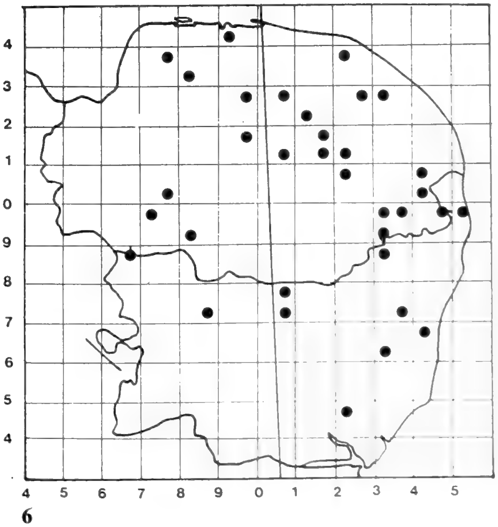
3


4
3
2
1
0
9
8
7
6
5
4
4 5 6 7 8 9 0 1 2 3 4 5

4


4
3
2
1
0
9
8
7
6
5
4
4 5 6 7 8 9 0 1 2 3 4 5

5


4
3
2
1
0
9
8
7
6
5
4
4 5 6 7 8 9 0 1 2 3 4 5

6

RUBUS SULCATUS VEST
E. Norfolk, a single clump in Hevingham Park (63/1.2.). Scarce in England from Berks. to Dorset, N. Devon and Herefs. Widespread in north-western and central Europe

RUBUS PLICATUS WEIHE & NEES
A plant of sandy commons in Norfolk, especially the eastern part of the county. Confined to a few similar sites in E. Suffolk. Absent from W. Suffolk. 75 v.cc., mainly in eastern England and Scotland. Ireland. Widespread in north-western Europe. (Fig. 3).

RUBUS ARRHENIIFORMIS W. C. R. WATS.
Dry heaths, usually growing among bracken. W. Norfolk, roadside by Hargham Heath (62/0.9.). E. Norfolk, Bryants Heath, Felmingham and Swanton Abbot Common (both in 63/2.2.), Crostwight Common (63/3.2.). E. Suffolk, Fritton Warren in one place (62/4.0.). British endemic. 17 v.cc. in England and Wales north to Cheshire and Derbys.

RUBUS VIGOROSUS P. J. MUELL. & WIRTG. (*R. AFFINIS* WEIHE & NEES PRO PARTE, NOM. ILLEG.)
Not infrequent in E. Norfolk. Three sites in E. Suffolk. Absent from the western part of both counties. I have seen Hind's sheet in **IPS** from Gorleston, labelled '*R. nitidus*' which Moyle-Rogers thought belonged here, but the leaf shape is very atypical. 26 v.cc. England and Wales north to Lincs. & S. Lancs. Widespread in north-western Europe. (Fig. 4).

SECTION *CORYLIFOLII* LINDL.

RUBUS CONJUNGENS (BAB.) ROGERS
Scattered throughout the region on all types of soils, ranging from sand dunes to boulder clay and fen silt. British endemic. 44 v.cc. in England, Scotland and Wales. Mainly southern and eastern, but north to Inverness. (Fig. 5).

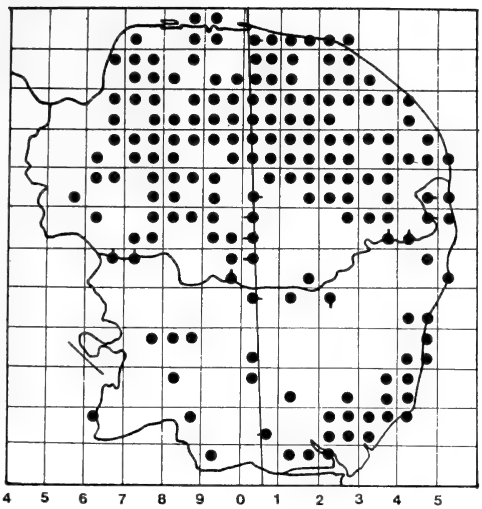
RUBUS EBORACENSIS W. C. R. WATS.
Under-recorded, as not named from East Anglia by E. S. Edees until 1977. Frequent in Norfolk, but appears to be less so in Suffolk, though occurs in both v.cc. in that county. Does not shun clay. British endemic. 32 v.cc. in England, Scotland and Wales. Mainly eastern, but extending west to Denbs. and north to Edinburgh. (Fig. 6).

RUBUS SUBLUSTRIS LEES
Apparently absent only from the Fens and some of the Suffolk clay. Often abundant on damp commons. All v.cc. in the study area. 57 v.cc. mostly in England and eastern Wales, but extending into Scotland at Kirkcudbright. Ireland. Widespread in Europe. (Fig. 7).

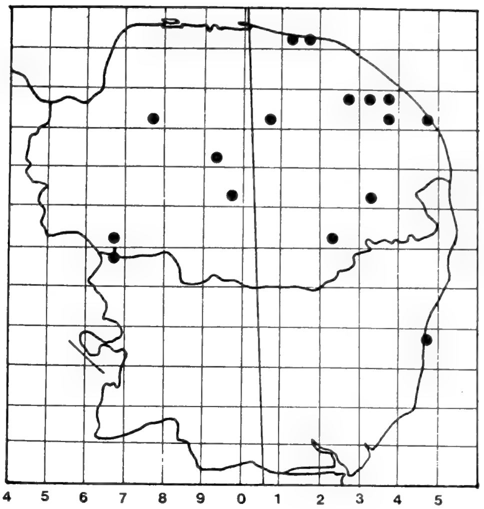
RUBUS NEMOROSUS HAYNE & WILLD. (*R. BALFOURIANUS* BLOXAM EX BAB.)
This species has a definite preference for peat and damp alluvial soils. Scattered in E. and W. Norfolk, especially in the Broads area and on the margins of the Fens. In Suffolk, only 2 sites. W. Suffolk, site unspecified (52/9.3.) (*J. D. Gray*, **LIVU**, comm. A. Newton). E. Suffolk, Dunwich beach (62/4.6.) (*A. L. Bull & J. Ironside-Wood*); Hind also gave Dunwich. 32 v.cc. in England, north to Cheshire. Ireland. Widespread in Europe. (Fig. 8).

RUBUS BABINGTONIANUS W. C. R. WATS.
Not found by the author. There are a number of sheets in **CGE** collected by B. A. Miles and others, from the area of Newmarket, e.g. Snailwell, Cambs. (52/6.6.), and one specimen of Miles' from Lawn Wood, Withersfield, W. Suffolk (52/6.4.).

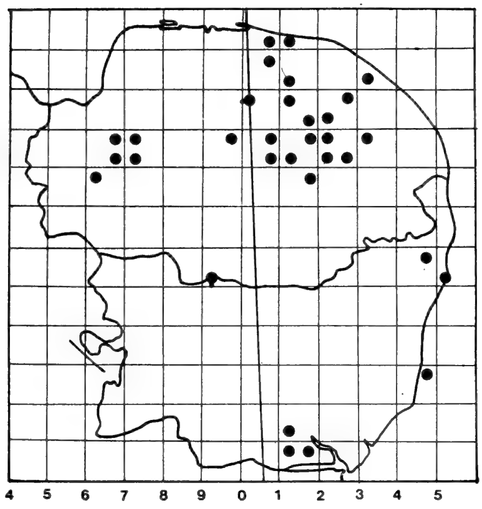
FIGURE 7. Distribution of *Rubus sublustris* Lees
FIGURE 8. Distribution of *Rubus nemorosus* Hayne & Willd.
FIGURE 9. Distribution of *Rubus gratus* Focke
FIGURE 10. Distribution of *Rubus platyacanthus* Muell. & Lefèv. ● Distribution of *Rubus sciocharis* Sudre ■
FIGURE 11. Distribution of *Rubus adspersus* Weihe ex H. E. Weber
FIGURE 12. Distribution of *Rubus nemoralis* P. J. Muell.


4 3 2 1 0 9 8 7 6 5 4
4 5 6 7 8 9 0 1 2 3 4 5

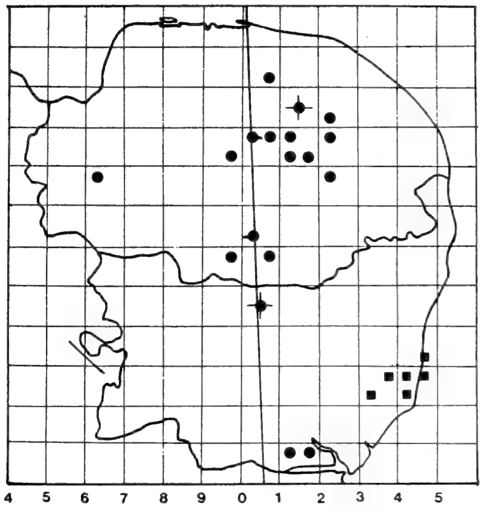
7


4 3 2 1 0 9 8 7 6 5 4
4 5 6 7 8 9 0 1 2 3 4 5

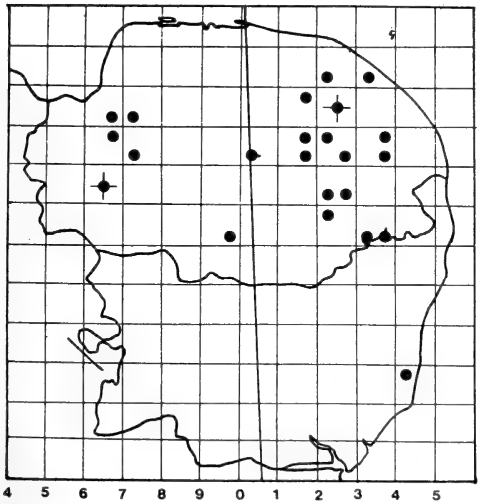
8


4 3 2 1 0 9 8 7 6 5 4
4 5 6 7 8 9 0 1 2 3 4 5

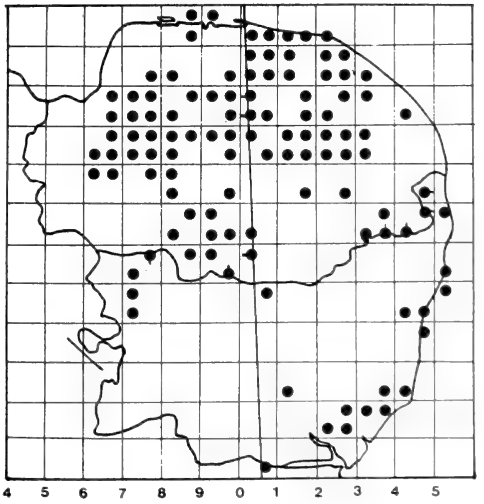
9


4 3 2 1 0 9 8 7 6 5 4
4 5 6 7 8 9 0 1 2 3 4 5

10


4 3 2 1 0 9 8 7 6 5 4
4 5 6 7 8 9 0 1 2 3 4 5

11


4 3 2 1 0 9 8 7 6 5 4
4 5 6 7 8 9 0 1 2 3 4 5

12

"*RUBUS FEROX* AGG."

There are a number of scattered localities for a plant which Watson saw in W. Norfolk at East Walton (53/7.1.), and named '*R. scabrosus*'. Among other densely-armed plants is one said to be "near *R. tuberculatus* but not identical with it", which is widespread, and another, chiefly from the W. Suffolk Breck, which is "near *R. britannicus*" (E. S. Edees pers. comm.). In addition there are five or six other members of the *Corylifolii* group in the study area, some of which are widespead, while others only occur very locally. None of these have been named.

SECTION *SYLVATICI* P. J. MUELL.

RUBUS GRATUS FOCKE

Most frequent in E. Norfolk, where it is locally dominant, e.g. Mousehold Heath, Norwich. Scarce in W. Norfolk and E. Suffolk, with only a single record for W. Suffolk. 23 v.cc. in England, north to S. Lancs. Scotland, Dunbarton and Kintyre. Wales, Glam. Ireland. Widespread in Europe. (Fig. 9).

RUBUS SCIOCHARIS SUDRE

E. Suffolk, mainly between the Rivers Alde and Deben. 21 v.cc. in England north to Lancs. and Yorks. Wales, Brecs. and Denbs. Widespread in Europe. (Fig. 10).

RUBUS NITIDIFORMIS SUDRE (*R. NITIDIOIDES* W. C. R. WATS.)

Rather rare. E. Norfolk, Billingford Wood (62/1.8.) (*A. L. Bull*). W. Suffolk, Polstead (52/9.4.) (*E. S. Edees*). E. Suffolk, Bentley Long Wood (62/1.3.) (*A. L. Bull*), Dodnash Wood (62/1.3.) (*A. L. Bull & E. S. Edees*), pathside by Sudbourne Great Wood (62/4.5.) (*E. S. Edees et al.*). 8 v.cc. in England, E. Sussex, Surrey, S. Essex, E. and W. Suffolk, E. Norfolk, W. Kent and Oxon. Widespread in Belgium and France.

RUBUS ADSPERSUS WEIHE EX H. E. WEBER

Typical, in the region, of damp, sandy commons, and almost confined to these. Scattered in E. and W. Norfolk. Two sites in E. Suffolk. 13 scattered v.cc. in England, Kent and Somerset, north to Cheshire. Widespread in Europe. (Fig. 11).

RUBUS PLATYACANTHUS MUELL & LEFÈV.

Scattered in E. and W. Norfolk, though often abundant where it occurs. E. Suffolk, only in Holbrook Park and Dodnash Wood (62/1.4.) (*E. S. Edees*). 37 v.cc. in England, Somerset to Kent north to S. Lancs. and Yorks. Eastern Wales. Widespread in Europe. This species and the last were formerly united under *R. carpinifolius* Weihe. (Fig. 10).

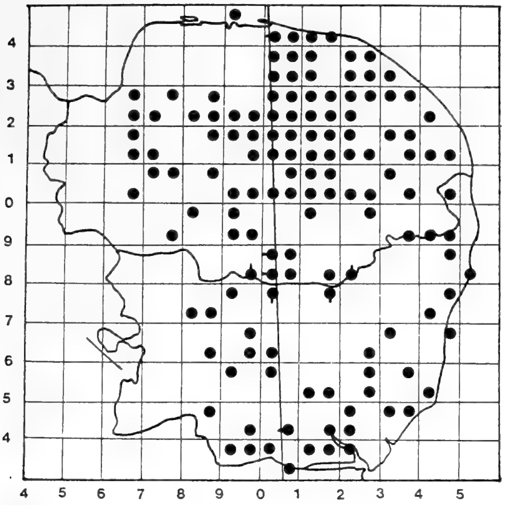
RUBUS NEMORALIS P. J. MUELL.

Widespread and frequent, especially on heaths and commons on sandy soil. Scarce on clay. 95 v.cc. in England, Scotland and Wales. Ireland. Widespread in Europe. (Fig. 12).

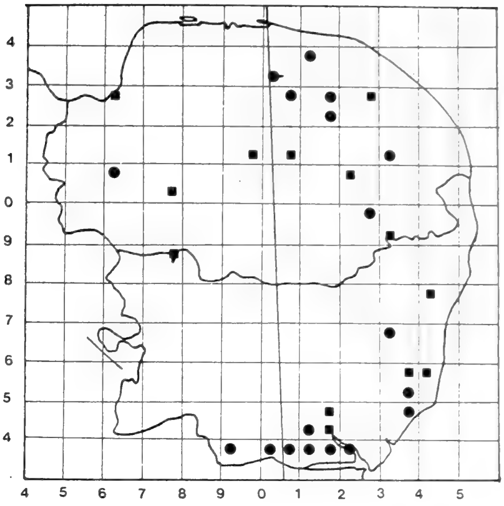
**RUBUS LACINIATUS* WILLD.

Origin uncertain. Doubtfully wild anywhere, though known as early as 1691. May have arisen as a natural sport, as at Outney Common, Bungay (q.v.). Occasionally met with in towns and villages where it has escaped from gardens, though rarely more than the odd bush. It is frequent where it is presumably bird sown in a conifer plantation at Cockley Cley, W. Norfolk (53/7.0.). At Outney Common, Bungay, E. Suffolk (62/3.9.), it is curiously the dominant bramble over several hundred acres. Found in all v.cc. in the study area. Naturalized in 37 v.cc. in England and Scotland. (Fig. 14).

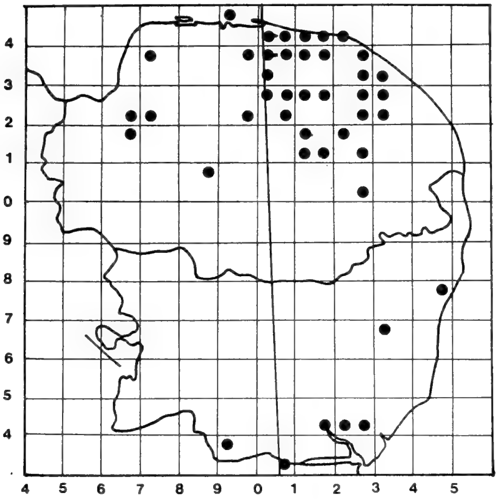
FIGURE 13. Distribution of *Rubus lindleianus* Lees
FIGURE 14. Distribution of *Rubus macrophyllus* Weihe & Nees ● Distribution of *Rubus laciniatus* Willd. ■
FIGURE 15. Distribution of *Rubus amplificatus* Lees
FIGURE 16. Distribution of *Rubus pyramidalis* Kalt. ● Distribution of *Rubus leptothyrsos* G. Braun ■
FIGURE 17. Distribution of *Rubus poliodes* W. C. R. Wats.
FIGURE 18. Distribution of *Rubus polyanthemus* Lindeb.



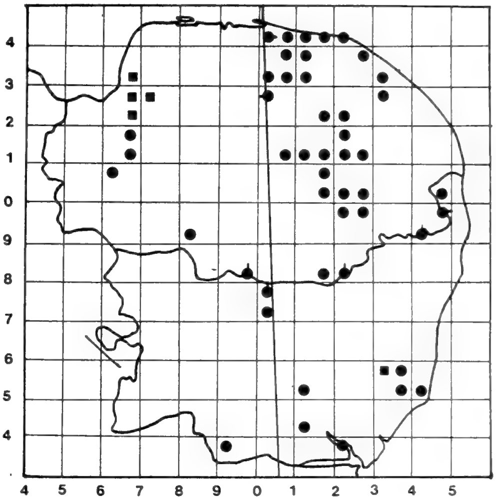
13



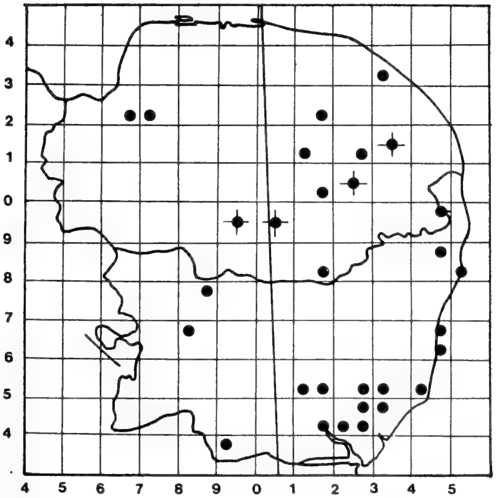
14



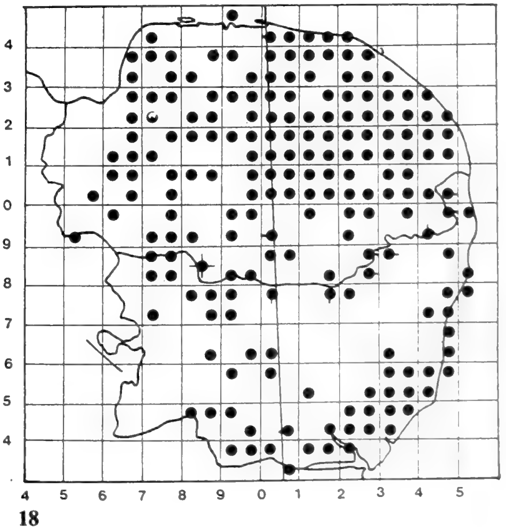
15



16



17



18

RUBUS LINDLEIANUS LEES

Common, not shunning clay, but strangely absent from much of the west of both counties. 82 v.cc. in England, Scotland and Wales. Ireland. Widespread in Europe. (Fig. 13).

RUBUS EGREGIUS FOCKE

Rare, E. Norfolk only. North Tuddenham Common (63/0.1.). Mousehold Heath, Norwich (63/ 2.0. & 2.1.). 5 v.cc. in England, Beds., Berks., Bucks. and Oxon. Widespread in Europe.

RUBUS MACROPHYLLUS WEIHE & NEES

Scarce in Norfolk, more frequent in southern Suffolk, though it occurs in all four vice counties. 29 v.cc. in England, north to Cheshire. Wales, Denbs. Scotland, Kintyre. Widespread in Europe. (Fig. 14).

RUBUS SUBINERMOIDES DRUCE

E. and W. Suffolk, close to the Stour valley. W. Suffolk, Stack Wood, Polstead (*E. S. Edees*), Hadleigh Heath and Groton Wood (*A. L. Bull*) (all in 52/9.4.), roadside near Hadleigh Heath, (*A. L. Bull*) (62/0.4.). E. Suffolk, Dodnash Wood, (*J. Ironside-Wood*) (62/0.3.), Chelmondiston, (*E. S. Edees et al.*) (62/2.3.). British endemic. 25 v.cc. in England, mainly south-eastern, north to Salop and Leics. Wales, Glam.

THURSFORD *RUBUS*

Looks superficially like the above. Included as it may be encountered by workers in the future. Specimens distributed to E. S. Edees, A. Newton and H. E. Weber. A. Newton comments on the very long, shaggy indumentum on the panicle, and states that he has not previously encountered a plant like it. Local endemic. E. and W. Norfolk, Thursford Wood (53/9.3.), Holmes Wood and Wood Severalls, Melton Constable (63/0.3.), Common Plantation, Aylmerton (63/1.3.), Old John's Wood, Gunton (63/2.3.). At each site, it is frequent to dominant. A specimen is lodged in **NWH** [No. 229.981(2)].

RUBUS AMPLIFICATUS LEES

Occurs in all v.cc. Especially common in E. Norfolk, scarce in Suffolk. Widespread species in England, Scotland and Wales, extending north to Fife. Ireland. (Fig. 15).

RUBUS PYRAMIDALIS KALT.

Common in E. Norfolk, scattered in other v.cc. 59 v.cc. in England, Scotland and Wales north to Ross. Ireland. Widespread in Europe. (Fig. 16).

RUBUS LEPTOTHYRSOS G. BRAUN (*RUBUS DANICUS* (FOCKE) FOCKE)

W. Norfolk, frequent in woods on or near the Sandringham estate. E. Suffolk, a single site at Campsea Ashe (62/3.5.). 5 v.cc. in England, Herefs., Leics. and Derbys. 26 v.cc. in Scotland, where it is frequent. Widespread in Europe. (Fig. 16).

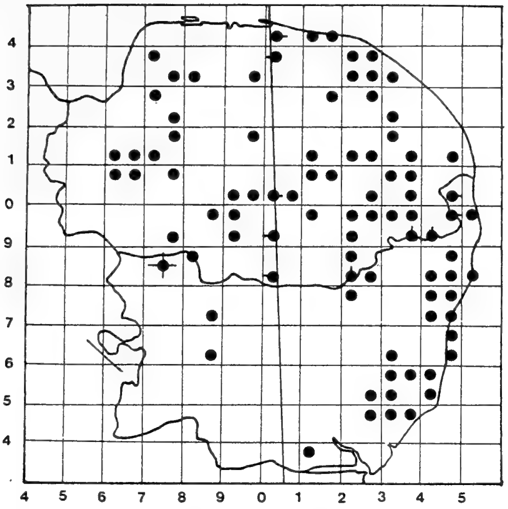
RUBUS POLIODES W. C. R. WATS.

E. Suffolk, especially common in the south-east and east of the v.c. Scattered in all the other v.cc. Regional endemic. 11 v.cc. in England, Herts. and Berks., north to Warks. and Norfolk. (Fig. 17).

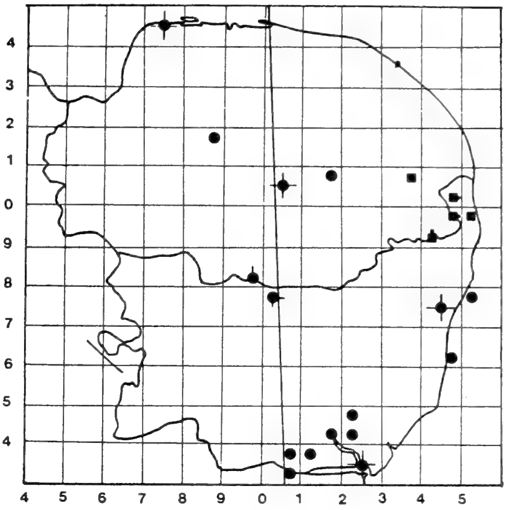
RUBUS SEPTENTRIONALIS W. C. R. WATS.

Four sites in W. Norfolk, Shouldham Thorpe Common and Broadmeadow Plantation, South Runction (both in 53/6.0.), Emily's Wood, Weeting (52/7.9.), Santon, south-eastern end of

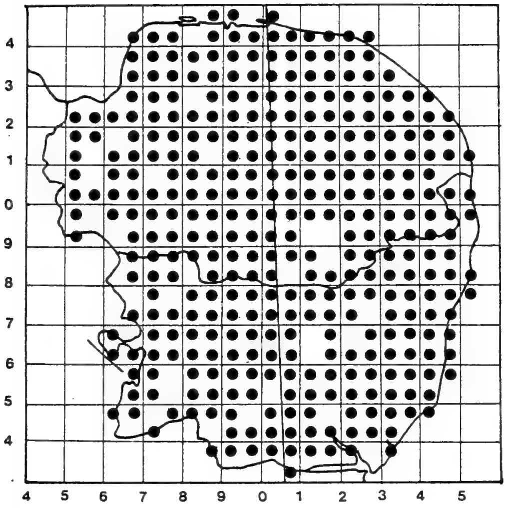
FIGURE 19. Distribution of *Rubus boudiccae* A. L. Bull & E. S. Edees
FIGURE 20. Distribution of *Rubus cardiophyllus* Muell. & Lefèv. ● Distribution of the Corton *Rubus* ■
FIGURE 21. Map showing the total coverage achieved, and the distribution of *Rubus ulmifolius* Schott.
FIGURE 22. Distribution of *Rubus procerus* P. J. Muell.
FIGURE 23. Distribution of *Rubus anglocandicans* A. Newton ■ Distribution of *Rubus sprengelii* Weihe ●
FIGURE 24. Distribution of *Rubus vestitus* var. *albiflorus* Boul.



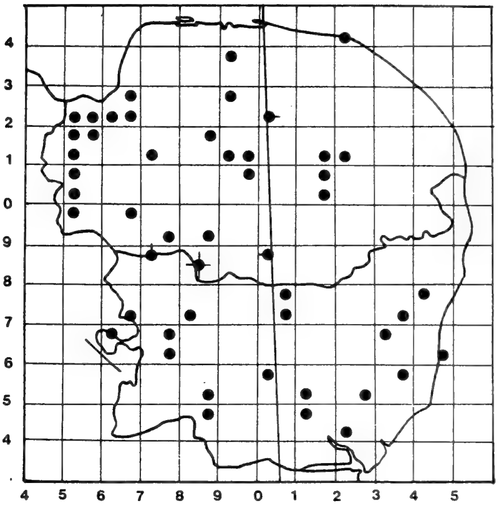
19



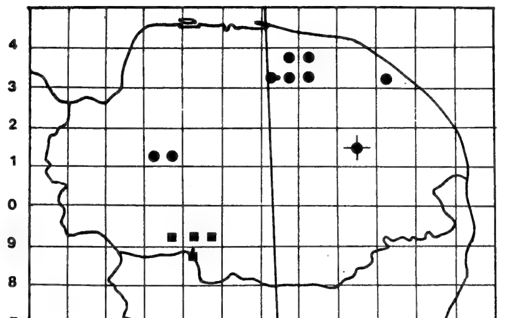
20



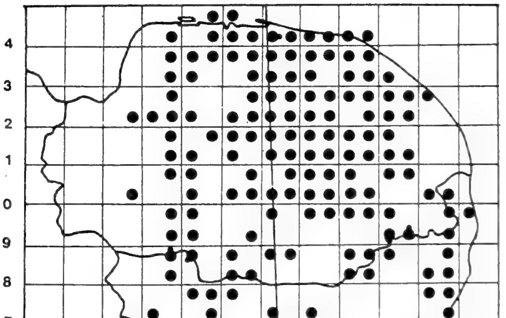
21



22



23



24

Grime's Graves (52/8.8.). England, Hants. and Dorset. Wales, Brecs. and Rads. Scotland, widespread in 25 v.cc. Widespread in Europe.

RUBUS INCURVATUS BAB.
E. Norfolk, Bard Hill, Salthouse, a single clump (63/0.4.). Widespread near endemic in British Isles. 25 v.cc. in England, Scotland and Wales. England, E. Kent, Cornwall to Lancs. Scotland, Hebrides only. Throughout Wales. Ireland. One locality in Denmark.

RUBUS POLYANTHEMUS LINDEB.
The second most abundant species in the region, though scarcer on clay than *R. ulmifolius*. 91 v.cc. in England, Scotland and Wales. Ireland. Widespread in Europe. (Fig. 18).

RUBUS CISSBURIENSIS BARTON & RIDDELSD.
E. Norfolk,Colney Hall Wood, a single colony (63/1.0.). Regional endemic. 15 v.cc. in England, Wilts. and Kent to Gloucs. and E. Norfolk.

**RUBUS ELEGANTISPINOSUS* (SCHUMACH) WEBER
E. Norfolk, Furze Covert, Rushall, a single bush (62/2.8.). E. Suffolk, frequent in three woods at Hoxne (62/1.7. & 2.7.). Introduced into Britain as a horticultural taxon, and naturalized in 10 v.cc. in England and Scotland.

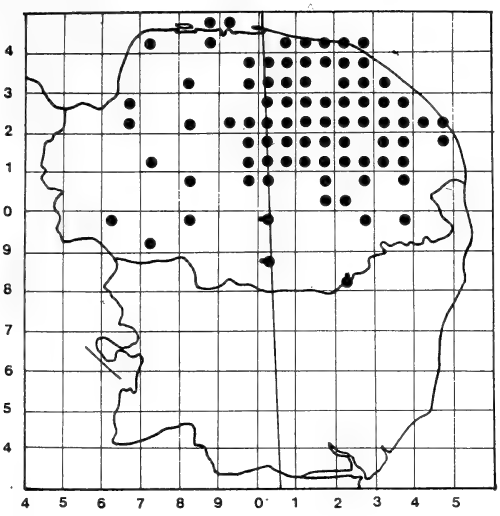
RUBUS BOUDICCAE A. L. BULL & E. S. EDEES
Common, especially on sandy and gravelly soils, less frequent on clay. E. and W. Norfolk, E. and W. Suffolk, N. and S. Essex. In the latter county, found at several sites near Colchester, and at Tiptree Heath and Danbury Common. There is a specimen in **NWH** collected in 1890 by J. D. Gray at Gt Horkesley, Essex. Regional endemic, the foregoing being the complete known distribution. Though S. Jermyn's specimen has not been seen, it is believed that *R. boudiccae* is the 'white Sylvatican' referred to in *Flora of Essex* (Jermyn 1974), as that occurs in the same areas as the present plant. (Fig. 19).

RUBUS CARDIOPHYLLUS MUELL. & LEFÈV.
Scarce in E. and W. Norfolk. More frequent in E. and W. Suffolk, especially in the south-east of that county. Due to confusion with the last named, only records collected by the present author, or sent him by A. Newton since the name *R. boudiccae* has been published, have been included. Material of this species has been examined in **CGE**, where one of B. A. Miles' specimens from Suffolk was of *R. boudiccae*, as was one of J. Ironside-Wood's in **BM**. 58 v.cc. in England, Scotland and Wales north to Ayrshire. Widespread in Europe. (Fig. 20).

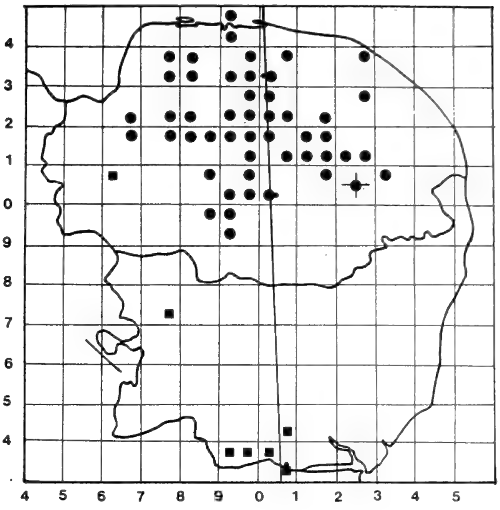
CORTON *RUBUS*
This is an unnamed local endemic, with a very attractive, intricate panicle, with milk white flowers borne on slender wiry pedicels. Frequent in north-eastern Suffolk and south-eastern Norfolk, and not likely to be missed by any batologist working the area thoroughly. There is a fine stand on the road junction just near the entrance to Blundeston prison, and on Corton cliffs. Specimens have been distributed to E. S. Edees, A. Newton and H. E. Weber, and to the herbarium at **NWH** [No. 229.981(1)]. (Fig. 20).

RUBUS ERRABUNDUS W. C. R. WATS.
A single bush beside the road within the National Trust's Minsmere Cliffs property on Dunwich Common, E. Suffolk (62/4.6.). 37 v.cc. in England, Scotland and Wales. England, scattered along

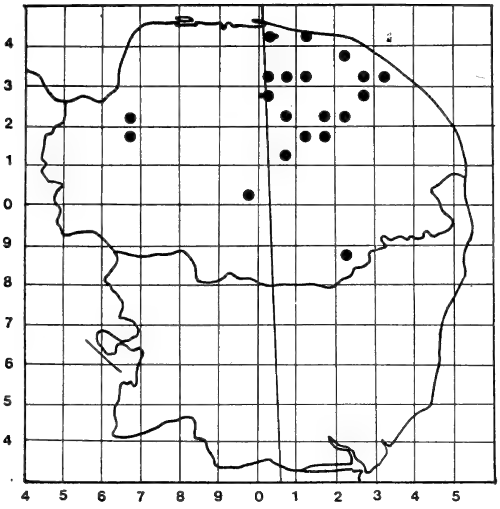
FIGURE 25. Distribution of *Rubus boraeanus* Genev.
FIGURE 26. Distribution of *Rubus criniger* (E. F. Linton) Rogers ● Distribution of *Rubus criniger*, ternate-leaved variant ■
FIGURE 27. Distribution of Rubus mucronulatus Bor.
FIGURE 28. Distribution of *Rubus leyanus* Rogers ● Distribution of *Rubus infestus* Weihe ex Boenn ■
FIGURE 29. Distribution of *Rubus radula* Weihe ex Boenn
FIGURE 30. Distribution of *Rubus echinatus* Lindl.



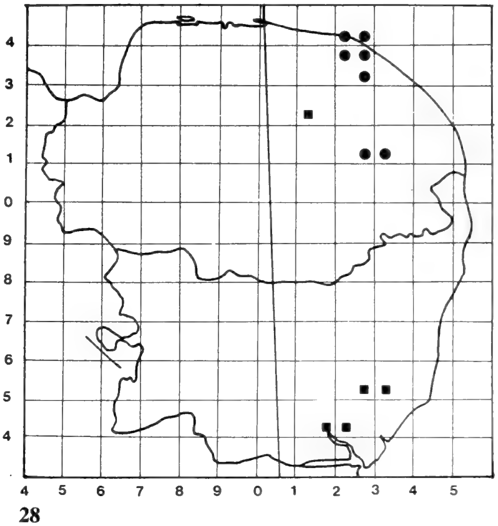
25



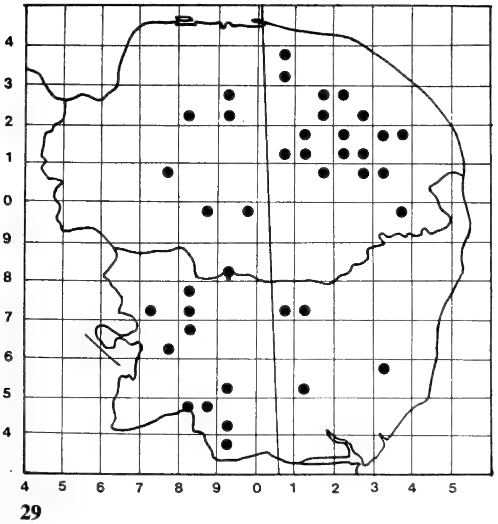
26



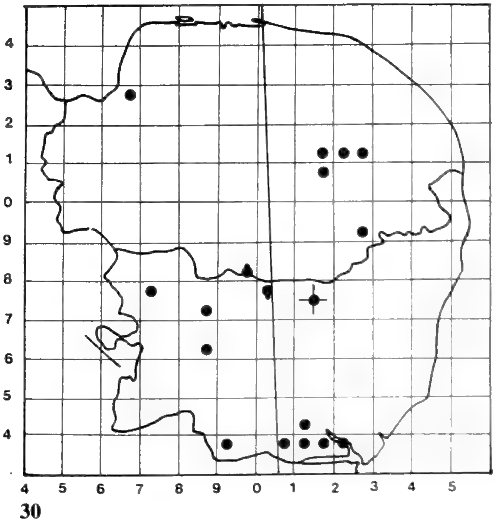
27



28



29



30

the south coast from W. Sussex to Devon, and especially in the north-west. North Wales. Frequent in south-western Scotland.

SECTION *DISCOLORES* P. J. MUELL.

RUBUS ULMIFOLIUS SCHOTT.

The commonest hedgerow blackberry. Found in all squares visited (Fig. 21). However, it is decidedly scarce on poor acid gravels. Dr E. A. Ellis has in his garden at Surlingham, E. Norfolk (63/3.0.) a plant with yellow prickles and pale amber fruit, which originated at Coston (63/0.0.). He also has a beautiful double form which came from Honing (63/3.2.). A fine plant of the latter variant grows on the lower slopes of St James' Hill, Mousehold Heath, Norwich (63/2.0.). In **IPS**, there is a specimen labelled '*Rubus fruticosus*' collected in 'Suffolk' by J. Davey in 1795. Abundant generally in most of England and Wales, but confined to the coast in northern England and Scotland. Ireland. Widespread in Europe.

RUBUS ARMIPOTENS BARTON EX A. NEWTON

W. Norfolk, Emily's Wood, Weeting (52/7.9.). E. Norfolk, Colney Hall Wood (63/1.0.). E. Suffolk, roadside colony in Eyke parish, 250 m south-west of Rendlesham church (62/3.5.). Endemic, widespread in England mainly south-east of a line Wilts./Salop/Leics., and also in N.E. Yorks.

RUBUS WINTERI P. J. MUELL. EX FOCKE

E. Norfolk, north side of Ketteringham Park Woods, by the roadside just west of the obelisk, where it is frequent. The large size of all parts, and especially the fruit, suggests that here it may be an escaped cultivar. Apart from this record, it is restricted in England to Notts., Derbys., Warks., and S.W. Yorks. Widespread in Europe.

**RUBUS PROCERUS* P. J. MUELL.

Naturalized cultivar. The 'Himalayan Giant' of nurserymen. Widely scattered in both counties, especially near towns. In the silt areas of the Fenland, where much soft fruit is grown, this species is rapidly becoming the most frequent bramble in roadside hedgerows. 44 v.cc. in England, Scotland and Wales, north to Perth. (Fig. 22).

RUBUS ANGLOCANDICANS A. NEWTON

There is a thriving colony over a few square miles of W. Norfolk Breckland, and a somewhat smaller area in E. Suffolk, where it is one of the dominant species on Foxhall Heath (62/2.4.) near the speedway stadium. Regional endemic in England, occurring mainly east of a line from Oxon to S.E. Yorks. (Fig. 23).

SECTION *SPRENGELIANI* FOCKE

RUBUS SPRENGELII WEIHE

A low growing plant of poor soils, scattered through the region, but most frequent on the moraine soils of the Cromer ridge. Absent from W. Suffolk. At Pond Hills, Hempstead, E. Norfolk (63/1.3.), there is a considerable white-flowered population. 52 v.cc. in England, Scotland and Wales. Ireland. Widespread in north-western Europe. (Fig. 23).

FIGURE 31. Distribution of *Rubus echinatoides* (Rogers) Dallman

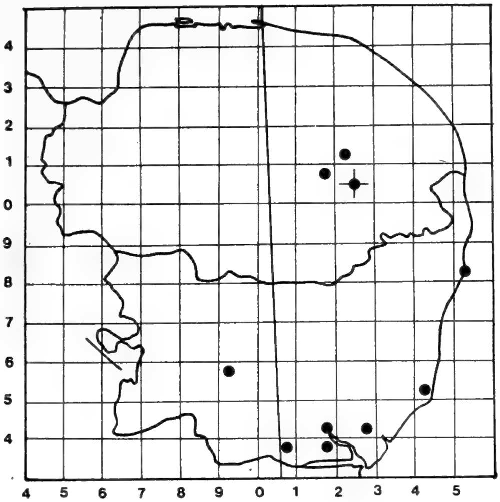
FIGURE 32. Distribution of *Rubus flexuosus* Muell., & Lefèv.

FIGURE 33. Distribution of *Rubus norvicensis* A. L. Bull & E. S. Edees ● Distribution of *Rubus adamsii* Sudre ■

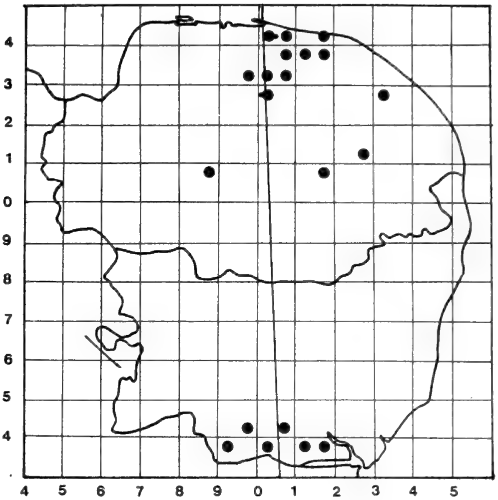
FIGURE 34. Distribution of *Rubus insectifolius* Muell. & Lefèv. ● Distribution of *Rubus iceniensis* A. Newton & H. E. Weber ■

FIGURE 35. Distribution of *Rubus rufescens* Muell. & Lefèv.

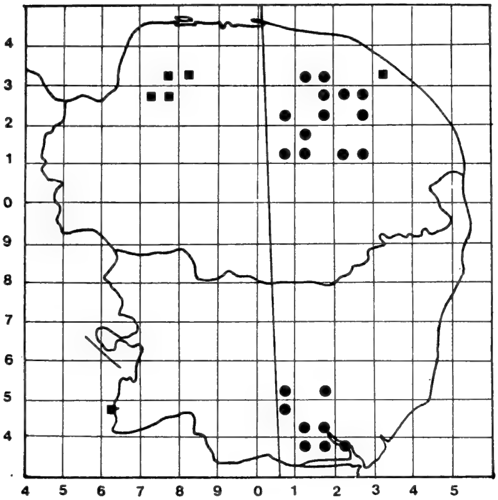
FIGURE 36. Distribution of *Rubus raduloides* (Rogers) Sudre



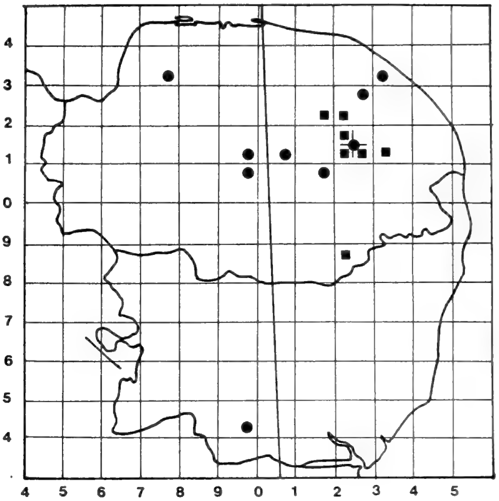
31



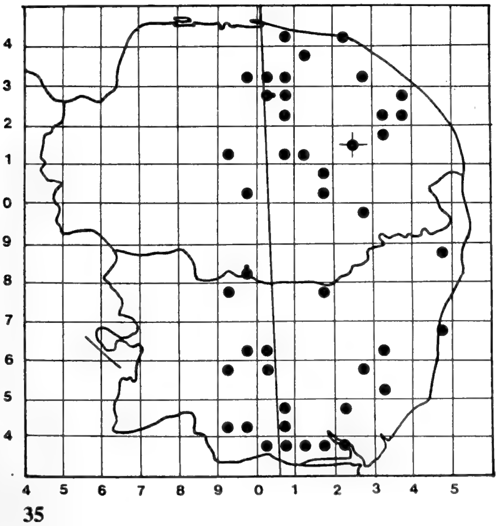
32



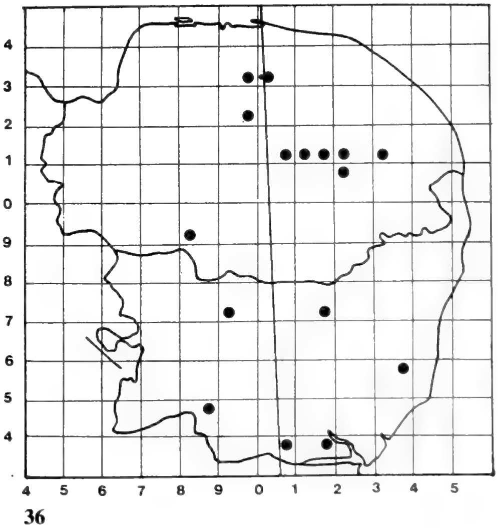
33



34



35



36

SECTION *APPENDICULATI* GENEV.

RUBUS SURREJANUS BARTON & RIDDELSD.

W. Norfolk, beside a forest ride to the north-west of Emily's Wood, Weeting (52/7.9.). E. Norfolk, Colney Hall Wood (63/1.0.), where it is frequent. Regional endemic in southern England, in 11 v.cc. south-east of a line from Somerset to Norfolk.

RUBUS VESTITUS WEIHE & NEES

The bright pink flowered form (var. *vestitus*) is scattered through the region at about two dozen sites. The var. *albiflorus* Boul. is especially abundant in woods, except in E. Suffolk. It is not unusual to find both forms growing side by side. 72 v.cc. in England, Scotland and Wales, north to Perth. Widespread in Europe. (Fig. 24).

RUBUS BORAEANUS GENEV.

Often abundant in Norfolk, especially in the north-eastern/central area in woods, on heaths and in hedgerows, becoming scarcer in the south and west. Oddly, there is no verified record for Suffolk, though it reappears again in Essex. 11 v.cc. in England, all near southern and eastern coasts except Herts. and E. Gloucs. Widespread in France. (Fig. 25).

RUBUS CRINIGER (E. F. LINTON) ROGERS

Frequent to abundant over a large area of central Norfolk. Absent from Suffolk. The species was first described from a Norfolk gathering by Linton, and in 1983 A. Newton collected it from the lectotype locality at Lexham near Swaffham. British endemic. 22 v.cc. in England, north to Man and Durham, but absent from many counties. (Fig. 26).

RUBUS CRINIGER, TERNATE-LEAVED VARIANT

This is suggested by A. Newton for an unnamed bramble which agrees in all respects with the species, other than the leaves being almost exclusively ternate, lacking the hairy anthers, and usually with a long ascending lower branch to the panicle. This taxon is abundant in N. Essex, v.c. 19, being one of the commonest plants in the Colchester area. It is also abundant along the Suffolk side of the Stour valley, with outlying colonies further north in W. Suffolk at Letch Moor, Icklingham, (52/7.7.), and in W. Norfolk at South Runcton (53/6.0.). (Fig. 26).

RUBUS MUCRONULATUS BOR.

Fairly frequent in north-eastern Norfolk, but scarce in the west. Absent from Suffolk. 45 v.cc. in England and Scotland, from Norfolk north to Orkney, but mainly in Scotland. Ireland. Widespread in Europe. (Fig. 27).

RUBUS LEYANUS ROGERS

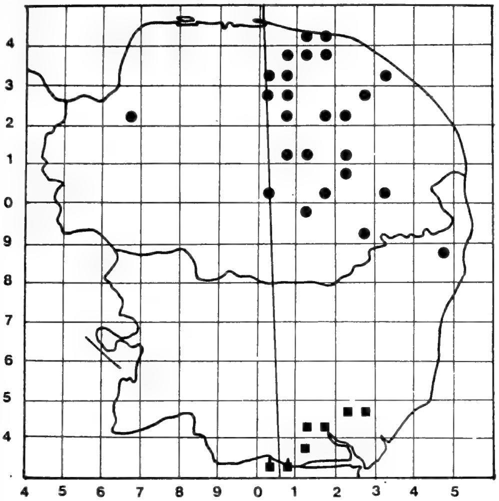
Chiefly in north-eastern Norfolk, and especially between Cromer and North Walsham, where it is locally frequent. This British endemic is mainly south-western. 26 v.cc. in England and Wales, Cornwall to Flint, Norfolk. (Fig. 28).

RUBUS INFESTUS WEIHE EX BOENN (*RUBUS TAENIARUM* LINDEB.)

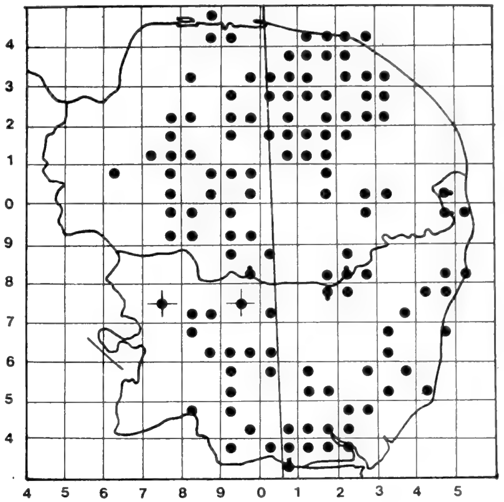
E. Norfolk, a small colony on Booton Common (63/1.2.) (*A. L. Bull*). E. Suffolk, Rushmere Heath (62/1.4.) (*A. L. Bull*), Foxhall Heath (62/2.4.) (*A. L. Bull & J. Ironside-Wood*), Bromeswell (62/2.5 & 3.5.) (*J. Ironside-Wood*). 21 v.cc. in England, two in Wales and 18 in Scotland, but mainly in northern England and Scotland, north to Inverness. Widespread in north-western Europe. (Fig. 28).

RUBUS RADULA WEIHE EX BOENN

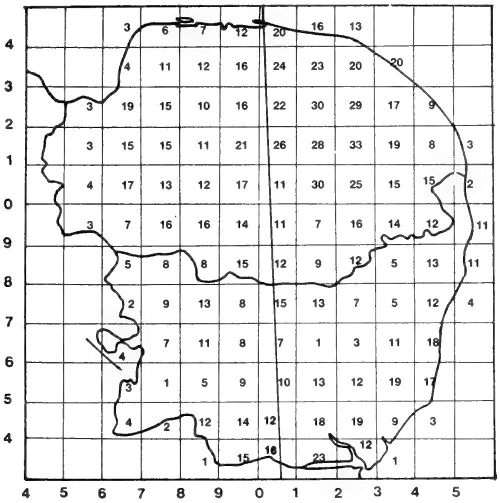
Scattered throughout the region on most soils. England and Scotland, where it occurs in 62 v.cc. but is most frequent in the east and north. Wales, Brecs. and Caerns. Ireland. Widespread in north-western Europe. (Fig. 29).



37



38



39

FIGURE 37. Distribution of *Rubus diversus* W. C. R. Wats. ■ Distribution of *Rubus hylocharis* W. C. R. Wats. ●

FIGURE 38. Distribution of *Rubus dasyphyllus* (Rogers) E. S. Marshall

FIGURE 39. Number of identified species in each 10-km square of the study area.

RUBUS ECHINATUS LINDL.

Seems to be distributed in disjointed areas–the Stour valley, the margins of Breckland, around Norwich, and in the region of Sandringham. 53 v.cc. in England and Wales, north to Yorks. Ireland. Widespread in France. (Fig. 30).

RUBUS ECHINATOIDES (ROGERS) DALLMAN

Only two sites in E. Norfolk, more widespread in Suffolk, especially in the south-east of that county. Widespread endemic occurring in 57 v.cc. in England, Scotland north to Perth, and in northern Wales. (Fig. 31).

RUBUS RUDIS WEIHE & NEES

W. Suffolk, Assington Thicks (52/9.3.) (*A. L. Bull & E. S. Edees*), Milden (52/9.4.) (*E. S. Edees*).

E. Suffolk, abundant in an orchard at the entrance to Mutford Wood, and in clearings in the wood itself (62/4.8.) (*A. L. Bull*). 25 v.cc. in England south-east of a line from Lincs. through Salop to Hants. Widespread in Europe.

RUBUS FLEXUOSUS MUELL. & LEFÈV.

Most frequent along the Cromer ridge, and along the Stour valley. Usually ternate-leaved, with a small zig-zag panicle. Occasionally in the open, adopting a more luxuriant form, with a large, intricate panicle and quinate leaves, as by the old railway track at Honing Common (63/3.2.). Not included on the map, is Groton Wood, Suffolk (52/9.4.), considered to be this species by A. Newton. The flowers are pure white, and too large, and the styles are almost purple, more reminiscent of *R. pallidus*, though the leaves are the wrong shape. 42 v.cc. in England and Wales, north to Derbys. and Northumb. Widespread in Europe. (Fig. 32).

RUBUS NORVICENSIS A. L. BULL & E. S. EDEES

Regional endemic. Frequent to abundant in E. Norfolk, from Norwich to north-west of Aylsham, in parts of southern E. Suffolk, and in N. Essex. I have collected it in the latter county from Layer de la Haye and Berechurch Common, south of Colchester. J. Ironside-Wood, whose collection in **BM** contains several specimens, considers that it can be found throughout the area from Chalkney Wood in the west, to St Osyth in the east. E. S. Edees collected the holotype from the lane to the north of Sloley church, E. Norfolk (63/2.2.). An isotype of *R. norvicensis* is lodged in **NWH** [No. 53.983(1)]. (Fig. 33).

RUBUS TRICHODES W. C. R. WATS.

E. Norfolk, Low Common, Gunton (63/2.3.). A regional endemic of south-eastern England. In E. and W. Kent, Surrey, Herts. and E. Norfolk.

RUBUS ADAMSII SUDRE

Locally frequent in north-western Norfolk, one site in north-eastern Norfolk. W. Suffolk, Lawn Wood, Withersfield (52/6.4.) (*B. A. Miles, A. Newton et al.*). A regional endemic in central and south-eastern England, from Wilts. and Kent to Staffs. and Leics. in 19 v.cc. (Fig. 33).

RUBUS PALLIDUS WEIHE & NEES

E. Norfolk, Sprowston Wood (formerly known as Church Wood) (*E. F. Linton, A. L. Bull et al.*), woodland at Thorpe St Andrews (*A. L. Bull*) (both in 63/2.1.). E. Suffolk, Holbrook Park (62/1.3.) (*E. S. Edees*). Omitted are plants from Langley, E. Norfolk (63/3.0.), which have very large leaves and green styles, and from W. Suffolk, from Birch Avery and Assington Thicks, both in Assington parish (52/9.3.). The latter specimens were very erect, very robust, and again have green styles, though leaf and panicle form agree with *R. pallidus*. 21 v.cc. in England and Wales, north to Yorks. Ireland. Widespread in Europe.

RUBUS GLAREOSUS ROGERS & MARSHALL

E. Norfolk, Pretty Corner, Sheringham (63/0.4.), where it is accompanied by a variety of unidentifiables. Seen in the field by E. S. Edees as well as the author. British endemic in south-eastern England, west to Somerset, with a large outlying colony in Brecs.

RUBUS ICENIENSIS A. NEWTON & H. E. WEBER

Locally abundant in the vicinity of Norwich, with a few outlying stations. Local endemic, E. Norfolk only. This is the plant referred to by E. F. Linton and subsequent workers as '*R. menkei* Weihe ap. Bluff & Fingerh'. Local records of *R. tereticaulis* P. J. Muell. should also be placed here. (Fig. 34).

RUBUS EURYANTHEMUS W. C. R. WATS.

W. Suffolk, (52/9.6.) (*W. H. Mills*, 1945, comm. A. Newton). An enquiry to **CGE** where the specimen is lodged, revealed that the site was 'between Bury and Rougham'. All woods in that area were searched during 1983 without success. E. Suffolk, Hoxne Wood (62/1.7.) (*A. L. Bull*), The Grove, Hoxne (62/2.7.) (*E. S. Edees et al.*). British endemic. 24 v.cc. in England, from Dorset and Kent north to Cheshire and Lincs. Wales, Rads.

RUBUS INSECTIFOLIUS MUELL. & LEFÈV.

Scattered in Norfolk, but locally abundant. Only one site in W. Suffolk, from Groton Wood (52/9.4.). 25 v.cc. in England north to Notts. and Derbys. Wales, Glam. Widespread in France. (Fig. 34).

RUBUS RUFESCENS MUELL. & LEFÈV.

Scattered to frequent in the eastern half of both counties, scattered in the west. 42 v.cc. in England, Somerset and Kent north to Lancs. and Yorks. Wales, Merioneth and Caerns. Scotland, Argyll. Widespread in France and Belgium. (Fig. 35).

RUBUS RADULOIDES (ROGERS) SUDRE

Commonest near Norwich, and in the Stour valley. There is a fairly widespread, white-flowered form in north-central Norfolk, confirmed by A. Newton. 40 v.cc. in England, eastern Wales, and southern and central Scotland. Widespread in Europe. (Fig. 36).

RUBUS PHAEOCARPUS W. C. R. WATS.

E. Suffolk, woodland margin by public footpath at Brightwell (62/2.4.). Perhaps endemic in south-eastern England. 12 v.cc., Wight to Kent, Beds., Bucks., Oxon and E. Suffolk. (North-western France?).

RUBUS LEIGHTONII LEES EX LEIGHTON

E. Suffolk, Somerleyton (62/4.9.) ("*L.C.*", August 1899, **OXF** comm. A. Newton). Searched for but not refound.

RUBUS MOYLEI BARTON & RIDDELSD.

E. Norfolk, Colney Hall Wood (63/1.0.). British endemic. 17 v.cc. in England, W. Kent to Herts., west to Somerset and Herefs. Wales, Glam., Brecs., and Rads.

RUBUS DIVERSUS W. C. R. WATS

E. Suffolk, often abundant between the rivers Deben, Orwell and Stour. 15 v.cc. in England north to Salop and Leics. Widespread in France. (Fig. 37).

SECTION *GLANDULOSI* P. J. MUELL

RUBUS MURRAYI SUDRE

W. Suffolk, Spelthorn Wood (52/8.4.) (*E. S. Edees*). Not refound. There is much of a *murrayi*-like plant in Spelthorn, and several other woods in that part of Suffolk, but no specimen sent to referees has yet been confirmed.

RUBUS HYLOCHARIS W. C. R. WATS.

Common in E. Norfolk, rare in the west. One record from E. Suffolk. British and Irish endemic. 41 v.cc. in England, Wales, Man and south-western Scotland. Ireland. (Fig. 37).

RUBUS DASYPHYLLUS (ROGERS) E. S. MARSHALL

Widespread and common in woods on most soils. 84 v.cc. in England, Scotland and Wales, north to Ross. Ireland. (Fig. 38).

RUBUS MARSHALLII FOCKE & ROGERS

E. Norfolk, Colney Hall Wood (62/1.0.). Regional endemic. 12 v.cc. in England from Kent to Hants. and Beds. to Herefs.

RUBUS ANGLOHIRTUS E. S. EDEES

E. Norfolk, Harleston (62/2.8.) (3rd August 1886, *E. F. Linton*, **LIVU**, comm. A. Newton). Cambs., Warren Hill, Cheveley (52/6.6.) (*A. L. Bull*). Regional endemic. 6 v.cc. in eastern England, from Rutland to Essex.

RUBUS PEDEMONTANUS PINKWART (*R. BELLARDII* WEIHE & NEES PRO PARTE, NOM. ILLEG.)

W. Suffolk, Spelthorn Wood (*E. S. Edees*), Stanstead Gt Wood (*A. L. Bull*) (both in 52/8.4.); Groton Wood (52/9.4.) (*A. L. Bull*). 16 v.cc. in England and Wales, scattered between Hants., Yorks. and Caerns. Widespread in Europe.

RUBUS "SERPENS" GROUP

E. Norfolk, Pond Hills, Hempstead (63/1.3.). E. Suffolk, roadside by woodland, Tattingstone (62/1.3.). As most of the panicle leaves are fringed at least part of the way round with stalked glands, E. S. Edees has suggested that this may prove to be the same plant as *R. leptadenes* Sudre, which is found in Bucks. For the time being, I am leaving it where placed by A. Newton, who describes the group as being of more trouble to batologists on the continent than in Britain.

RUBUS LINTONII FOCKE EX BAB.

E. Norfolk, Mousehold Heath, Norwich (63/2.0.& 2.1.), Sprowston (63/2.1.) Haveringland Gt Wood, and Hevingham Park (63/2.2.). Disjunct endemic, occurring in Herts., E. Norfolk and Staffs.

In addition to the above there are quite a number of unnamed local endemics. There are plants restricted to a limited area, perhaps a single wood or common, and are unlikely to be named in the foreseeable future though apparently 'good' species with viable fruit and distinctive characteristics.

There are also a number of hybrids, usually more or less sterile, and showing characteristics of either *R. caesius* or *R. ulmifolius*. One identifiable sterile hybrid which is seen from time to time, is *R. ulmifolius* × *R. vestitus*. No attempt has been made to map any hybrids.

DISCUSSION

It has been suggested that batologists find most brambles in the area in which they live. Certainly, living ten miles west of Norwich, the best areas are nearby. On the other hand, the author was born on the mid-Suffolk clay, in the third largest parish in that county, and lived there for many years. The only species occurring there are *R. caesius* and *R. ulmifolius* (see Fig. 39).

On a national basis, more species of bramble occur in areas of high rainfall, but in East Anglia the influence of rainfall distribution does not seem significant. The monthly rainfall totals for Norfolk have been studied, and it was discovered that the wettest area was consistently round Bradenham in the west of the county, where the land tops the 100 m contour. Here, the soil is boulder clay which, even in areas where bramble species are more plentiful, usually has much lower densities of species than do sands and gravels. In East Anglia at least, where these latter soil types outcrop, as they do haphazardly where they were deposited by the retreating ice fields after the last glaciation, are the areas of highest species density in the region. Such deposits are usually too localized to show up on any geological maps.

The richest area for brambles in Norfolk is in the vicinity of Norwich. Mousehold Heath and Sprowston were formerly part of a much larger heath stretching eastwards almost to Woodbastwick, a distance of almost seven miles. To the west and north-west of the city, Colney Hall Wood, and the steep sided Wensum valley as far as Ringland Hills, are all parts of a glacial outwash plain composed of gravelly sands capped by coarse flinty gravels (Funnell 1975). Again rich in brambles, is Salthouse Heath on the Cromer ridge, itself a glacial moraine. Conversely, the boulder clays, laid down beneath actively moving glaciers, are among the poorest soils for brambles other than *R. ulmifolius*.

The richest areas in Suffolk are all on the 'Sandlings', down the coastal belt, and especially in the Ipswich area, and between the rivers Alde, Deben, Orwell and Stour, a general area well known to geologists for its outcrops of 'Red Crag'.

The sands of Breckland in the west of both counties, and extending into Cambs., are rather poor, though there has been a dramatic increase in the numbers of species and density of brambles in recent years, with the growth of the state forests. The reason for this is not difficult to find, when one considers the large flocks of migrant members of the Thrush tribe. These quickly clear any remaining blackberries when they arrive in early October, and then roost in the young plantations. At Cockley Cley, in a remote plantation, half a dozen species include a sprinkling of bushes of the cultivated *R. laciniatus*. All must have arrived by the agency of birds, as the former heaths of Breckland were devoid of any cover apart from scrubby pine belts supporting only stunted Elder.

A similar increase in bramble species has occurred on the coast at Holkham, where, in the late 19th century, the then Earl of Leicester planted Corsican Pine on the grey dunes from Wells to a point about a mile to the west of Holkham Gap. Today, up to ten species of bramble are abundant in the afforested dunes, while the grey dunes, which continue westward past the Burnhams to Scolt Head, have none, other than the odd stunted bush of *R. ulmifolius*.

Many 'single bush' occurrences must indicate recent arrivals with avian assistance, such as *R. errabundus* within 100 m of the edge of Dunwich cliffs in Suffolk, and *R. incurvatus* on top of Bard Hill, Salthouse, looking down on the north Norfolk coast. Similarly, a single clump of *R. sulcatus* in the woods at Hevingham Park, Norfolk, is more likely to have arrived there from north-western Europe, where it is frequent, than from the remote and scattered colonies in south-western England.

Reverse migration can also occasionally take place, for which there is plenty of evidence to be found in the archives of the British Trust for Ornithology at Tring. Adverse weather conditions forcing a flock of birds north again after they had fed well, say, on a Surrey common, might well account for 25% of the bramble species found in Colney Hall Wood. Of 20 species found in the wood, five are scarce north of the Thames and, of these, three occur nowhere else in the study area. These latter species are not represented by single bushes, but rather by small colonies of bushes. They may originally have started as single bushes, or several seeds may have arrived at the same time, brought, perhaps, by a flock of birds.

It appears that new species of bramble are still being brought into the area, chiefly by avian transport, and that such a process has been happening ever since the last ice age. Species such as *R. pergratus*, *R. sulcatus*, *R. incurvatus*, *R. errabundus*, and *R. phaeocarpus*, which are represented by single bush occurrences, would appear to be recent introductions. Species such as *R. cissburiensis*, *R. winteri*, *R. trichodes*, *R. glareosus*, *R. moylei* and *R. marshallii*, represented by small colonies of bushes, would appear to be of somewhat earlier introduction. There are also a number of species with a somewhat wider distribution, but of limited range, which probably represent even older introductions. In this latter group of very early colonists could be included *R. sciocharis*, *R. egregius*, *R. leptothyrsos*, *R. elegantispinosus*, *R. leyanus* and perhaps even *R. boraeanus*, which is very abundant in north-eastern Norfolk, becoming scarcer in the west and south of the county, and actually disappearing within sight of the Suffolk boundary, the next colonies being in Essex.

Newton (1980) has included Norfolk and northern Suffolk in the North Sea Florula, which also includes north-eastern England and Scotland. Southern Suffolk is in an overlap area between the Midland and Southern Florula, and the North Sea Florula. In addition to widespread species, it is of interest to note that the study area lays claim to nine species from the North Sea Florula, eight from the Midland and Southern Florula, most of which are found in Norfolk, two, *R. incurvatus* and *R. leyanus*, from the Western Florula, and *R. errabundus* from the Irish Sea Florula.

Although 100% coverage of the study area has not been achieved, it was felt that the survey had gone on long enough to give a moderately accurate picture of the number of species to be found in the region and their distribution. If the publication of this paper encourages batologists in other regions to follow suit, then it will have been worthwhile. In any event, it has been a fascinating study, and the author now knows where virtually every piece of woodland and common land in the study area is to be found!

ACKNOWLEDGMENTS

The author would like to acknowledge a debt of gratitude to E. S. Edees for many years of help and encouragement in the field, with identifying pressed specimens, and with the preparation of this article; also to A. Newton who has proffered much helpful advice, identified specimens, supplied all the national and international distribution data and sent in many records that he has encountered in various herbaria; to Professor H. E. Weber, for commenting on specimens sent to him for examination; to the keepers of the Herbaria mentioned in the text for facilities freely given to examine specimens at leisure; to P. W. Lambley of Norwich Castle Museum for encouragement, especially with this paper, and also for drawing the original map on which the distribution maps are based; to J. Ironside-Wood for many records from Suffolk, and help with the Essex distributions of *R. norvicensis*; to C. Roper of Ipswich for preparing the distribution maps; to one of the editors of Watsonia for much help and advice on the organization of the facts; to all the landowners who ungrudgingly gave me access to their woods, and with apologies to those into whose woods I may have inadvertantly strayed! Finally, thanks to my wife who has tolerated my fascination with such thorny problems, both indoors and out, for such a long period.

REFERENCES

Bull, A. L. & Edees, E. S. (1980). A new bramble from East Anglia. *Watsonia*, **13**: 121–2.

Bull, A. L. & Edees, E. S. (1983). Another new East Anglian bramble. *Watsonia*, **14**: 411–2.

Edees, E. S. (1974). The Brambles of Suffolk. *Suffolk Natural History*, **16**: 338–346.

Funnell, B. M. (1975). The origin of Mousehold Heath, Norwich. *Trans. Norfolk Norwich Nat. Hist. Soc.*, **23**: 251–6.

Jermyn, S. T. (1974). *Flora of Essex*. Colchester.

Newton, A. (1980). Progress in British *Rubus* studies. *Watsonia*, **13**: 35–40.

Newton, A. & Weber, H. E. (1977). *Rubi* common to the British Isles and north-western continental Europe. *Watsonia*, **11**: 380–2.

Petch, C. P. & Swann, E. L. (1968). *Flora of Norfolk*. Norwich.

Simpson, F. W. (1982). *Simpson's Flora of Suffolk*. Ipswich.

Watson, W. C. R. (1958). Rubi *of Great Britain and Ireland*. Cambridge.

(*Accepted March 1984*)

The updated distribution of maritime species on British roadsides

N. E. SCOTT

Department of Plant Biology, The University, Newcastle-upon-Tyne, NE1 7RU

ABSTRACT

Maritime species newly reported from roadsides are *Atriplex littoralis, Armeria maritima, Bupleurum tenuissimum, Desmazeria marina, Elymus pycnanthus, Halimione portulacoides, Juncus gerardii* and the fungus *Agaricus bernardii*. Previously known species have continued to spread. Of these the most successful are those adapted to a disturbed habitat, *Puccinellia* spp., *Spergularia marina, Cochlearia danica* and *Parapholis strigosa*. The most widespread species, *Puccinellia distans*, continues to spread but is confined to northern and eastern England where roadside soils are more saline because of the colder and drier climate. Other maritime species occur on roadsides near to the eastern coast. Invasion appears to originate from local coastal sites with seeds being carried on vehicles to roadsides.

INTRODUCTION

The distribution of maritime species on British roadsides was described by Scott & Davison (1982). In response to that paper the author has received many further reports so that it is now possible to present updated distribution maps and to reconsider some of the questions raised in the 1982 report.

NEW RECORDS

PUCCINELLIA

Since the publication of the last distribution map for *Puccinellia distans* (Jacq.) Parl. on roadsides (Scott & Davison 1982) there have been several new records of this species sent to the authors and several reports have appeared in the literature. The updated map (Fig. 1) includes these new records. *Puccinellia distans* is now known on two roads in Cumbria: on the A6 as it crosses Shap Fell (H. Robbins pers. comm.) and on the M6 near Penrith (Halliday 1983). It has also been reported from Berkshire on the M4 east of Oxford (H. J. Bowman pers. comm.), from Hampshire on the A30 and at an interchange on the M3 (G. Kitchener pers. comm.), from Sussex on the A272 (J. Badmin pers. comm.) and from Surrey at intersections on the M23 and M25 (G. Kitchener pers. comm.). In the vice-counties in which it was already known, it has continued to spread. This is particularly so in the vice-counties of north-eastern England, Kent (Kitchener 1983) and East Anglia, where it is now known on several roadsides in Norfolk (Daniels 1984) and on the A12 between Woodbridge and Chelmsford.

In W. Kent, v.c. 16, Kitchener (1983) has also found *P. fasciculata* (Torr.) Bicknell and *P. rupestris* (With.) Fern. & Weatherby. Thus, with the records for *P. maritima* (Huds.) Parl. for north-eastern England (Mathews & Davison 1976), there are now four members of this genus on British roadsides. The report of *P. fasciculata* for north-eastern England (Scott & Davison 1982), however, was incorrect. This report was the first record of this species north of Norfolk and so brought into question the conclusion that the maritime species had been introduced from local coasts. Morphologically, the original specimen was very like *P. fasciculata* (for instance it had lemma lengths of 2·2–2·3 mm) but as identification of the plant was not easy, a cytological investigation by D. A. Stevens and subsequently by C. A. Stace was undertaken. They showed that the chromosome number did not correspond with that for *P. fasciculata*.

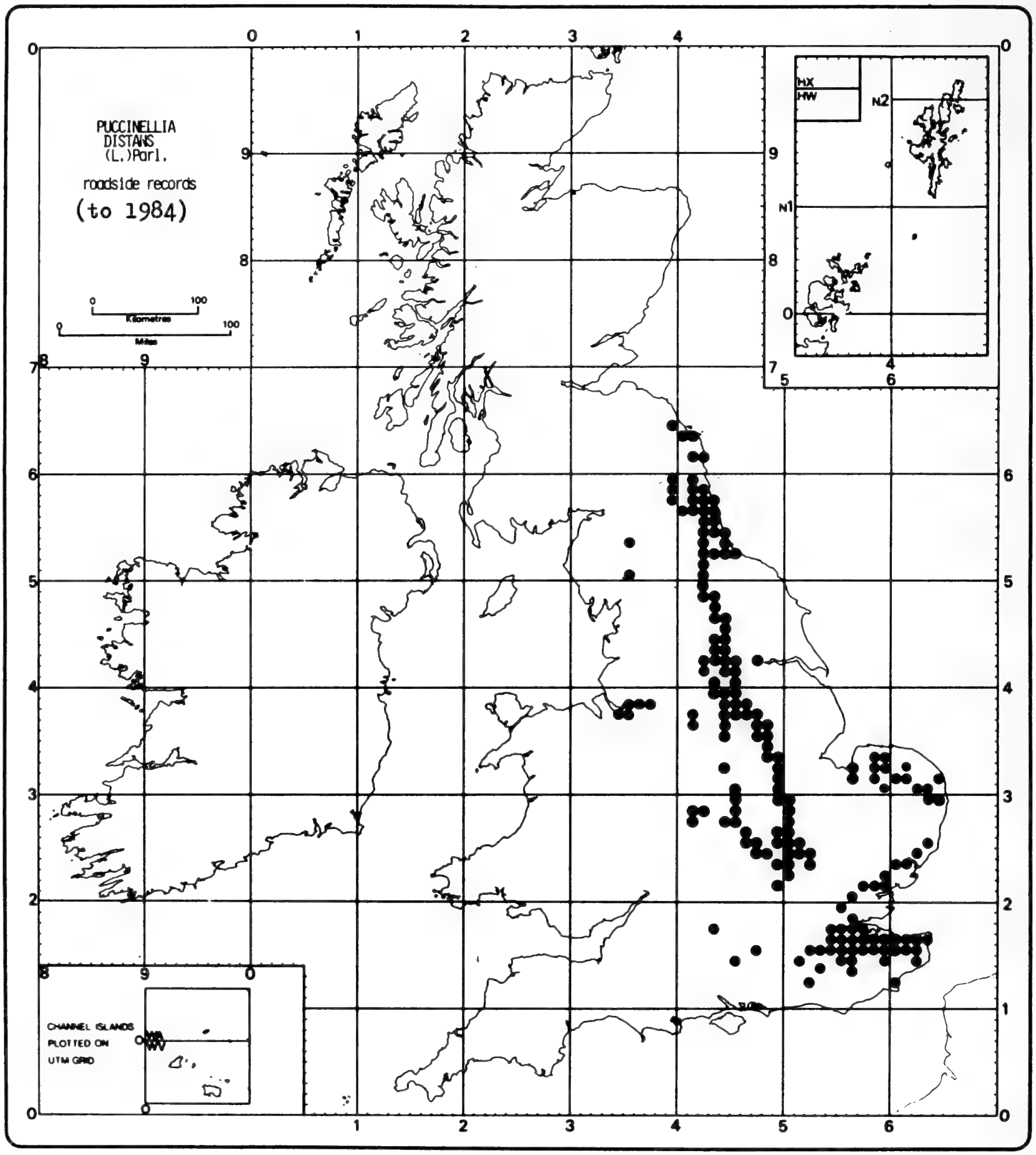


FIGURE 1. The distribution of *Puccinellia distans* on British roadsides, up to 1984.

C. A. Stace (pers. comm.) reported that the specimen had a chromosome number of 2n=51, that meiosis showed irregularity but not to the degree normally found in hybrids in this genus and that seed set appeared to be good. He tentatively concluded that the specimen was a hybrid between *P. distans* and *P. maritima*, possibly a backcross to *P. maritima*.

SPERGULARIA

Since the publication of the distribution maps in Scott & Davison (1982), *Spergularia marina* (L.) Griseb. has made the most impressive expansion in north-eastern England, now occurring in 23 1 km-squares compared with 11 in 1981. There are also records for E. Norfolk, v.c. 27 (Daniels 1984) and W. Kent, v.c. 16 (Kitchener 1983) as well as the record reported earlier from E. Kent, v.c. 15 (Scott & Davison 1982). This species has also been recorded from the A833 in Easterness, v.c. 96, by C. S. V. Yeates (pers. comm.), which is the first report of a maritime species occurring on a roadside in Scotland that appears to be associated with the use of de- icing salt. C. S. V. Yeates also reported, however, that the population is now extinct due to road improvements. In contrast *Spergularia media* (L.) Presl is still confined to the sites in which it was known in 1975 (Mathews & Davison 1976).

ATRIPLEX

A. littoralis L. has recently been identified from roadsides in north-eastern England. It is present at several sites on the A1 (e.g. GR 45/182.873 and 45/229.756). This species is common on local coasts, where it can be easily distinguished from other *Atriplex* species but, on the roadside, identification is more difficult as this genus is frequently heavily infected with insect galls. It is possible, therefore, that this species has been present on the roads of north-eastern England for some time. It has also recently been found on the A1 in S.W. Yorks., v.c. 63 (C. S. V. Yeates pers. comm.).

COCHLEARIA

The roadside populations of *Cochlearia danica* L. in East Anglia have continued to increase (Hyde *et al.* 1981, 1982, 1983), particularly on the A45, along which it now goes 70 km inland to Cambridgeshire. This species has also been found on the roadsides of W. Kent, v.c. 16 (Kitchener 1983) and Surrey, v.c. 17. In Surrey it was first recorded in 1968 by D. W. Baldock on the A3. This colony has since expanded and others have appeared up to 9 km away on the same road (A. C. Leslie pers. comm.).

PARAPHOLIS

Parapholis strigosa (Dumort.) Hubbard has recently been discovered in three vice-counties. In W. Kent, v.c. 16 (Kitchener 1983), on the A1065 in W. Norfolk, v.c. 28 (G. Kitchener pers. comm.) and on the A12 in E. Suffolk, v.c. 25 (E. Hyde pers. comm.). In W. Kent, *P. strigosa* is now one of the commonest maritime species on roadsides (G. Kitchener pers. comm.).

ASTER

All the original (1975) populations of *Aster tripolium* L. in north-eastern England (Scott & Davison 1982) are now extinct but others have recently appeared on different stretches of road. This seems to confirm the suggestion made in the previous paper that *A. tripolium* populations are short-lived, being prevented from setting seed by mowing, and that this species is being reintroduced continually. *Aster tripolium* is on the banks of the River Tyne close to Newcastle and this may be the seed source reaching roadsides. One of the newly discovered populations is on the A6085 in S. Northumb., v.c. 67 (GR 45/186.645) and only 400 m from a riverside site. *Aster tripolium* has also been recorded on the roadsides of E. Kent, v.c. 15 (Kitchener 1983).

OTHER GENERA

The list of species discovered by G. Kitchener on the roadsides of W. Kent is extensive (Burton 1983; Kitchener 1983 and pers. comm.). Besides the species already mentioned there are also *Armeria maritima* (Miller) Willd., *Bupleurum tenuissimum* L., *Desmazeria marina* (L.) Druce, *Elymus pycnanthus* (Godron) Melderis, *Halimione portulacoides* (L.) Aellen and *Juncus gerardii* Loisel. Two of these species have also been found elsewhere: *Juncus gerardii* now occurs on the A146 in E. Norfolk, v.c. 27 (Daniels 1984) and *Armeria maritima* on the A40 near Oxford (v.c. 23) (H. J. Bowman pers. comm.) and on the A12 in E. Suffolk, v.c. 25 (G. Kitchener pers. comm.).

Another recent discovery is the fungus *Agaricus bernardii* (det. D. A. Reid, R.B.G., Kew) on the A696 in north-eastern England. This species is usually associated with saltmarshes but has been found on saline roadsides before (Phillips 1981).

All of these new records have been included with records from the 1982 report in Fig. 2. This shows the current distribution of all maritime species on Britain's roadsides other than *Puccinellia distans* and those records considered as being unrelated to the use of salt. This figure demonstrates how these records are tending to occur on roadsides near to the eastern coast.

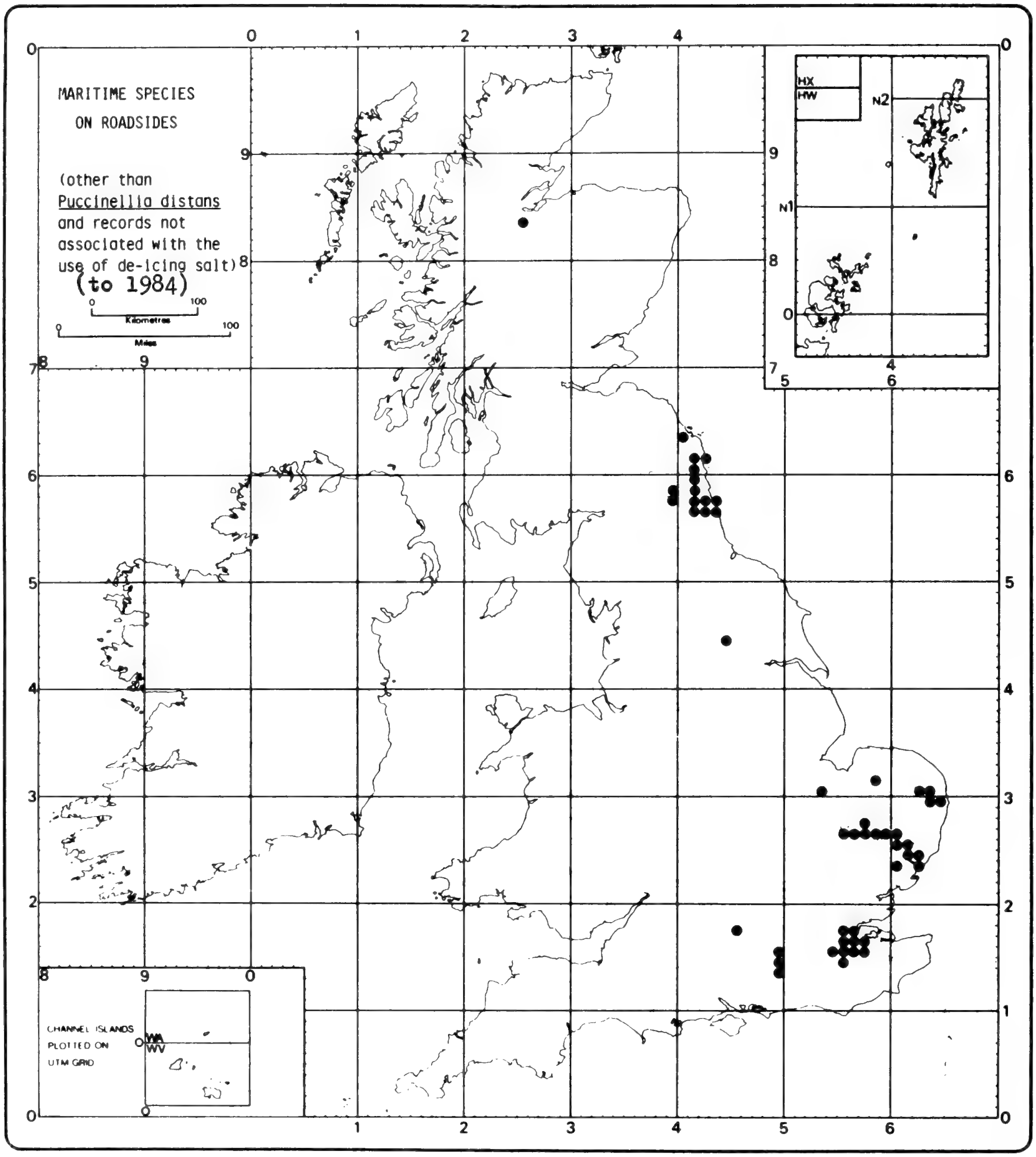


FIGURE 2. The distribution of maritime species, other than *Puccinellia distans* and records unlikely to be associated with the use of de-icing salt, on British roadsides, up to 1984.

DISCUSSION

DISPERSAL

The new information on species distribution goes some way to confirming some of the principal conclusions drawn in Scott & Davison (1982). An analysis of rates of spread then showed that the most successful species tended to be those adapted to a disturbed saline environment. In north-eastern England, *Puccinellia distans* and *Spergularia marina* continue to spread the most rapidly. Elsewhere in Britain it is now noticeable that species similarly adapted to a disturbed habitat are also spreading rapidly, notably the annuals *Cochlearia danica* and *Parapholis strigosa*, as well as *Puccinellia* spp.

Puccinellia distans continues to be confined to the north and east of England and Wales (Fig. 1). This distribution is probably due to differences in the use and effect of de-icing salt in different parts of the country. In the west and south the low use of salt is due to the lower incidence of frost whilst the salinity of roadside soil is reduced further in the west by the higher rainfall (Thompson *et al.* 1979). The continued absence of this species from Scotland is more puzzling, for although less salt may be used than in northern England it is still enough to cause damage to verges on some of the main roads, and for *Spergularia marina* to have been found.

It was also suggested in Scott & Davison (1982) that seed was being distributed by vehicles. Evidence showing how the seed of these species is swept along in vehicular slipstreams has been described by Scott (in press). Amongst the new records for *Spergularia marina* and *Puccinellia distans* in north-eastern England is one each for isolated sites some distance inland. These are both near places regularly visited by the vehicle used for experiments on maritime plants, so that it is considered that they were inadvertently spread by the author. The site for *Puccinellia distans* is on a road in the author's village, Elsdon (GR 35/936.934), and for *Spergularia marina* it is near a salt dump on the A68 (GR 35/935.777) which is used as a source of salt for experiments. Both populations are approximately 40 km inland and 20 km from the nearest other population. These records are evidence that seed can be carried on vehicles. They also show how easily botanists can be unconsciously responsible for the spread of opportunist species.

ORIGINS

In Scott & Davison (1982) it was pointed out how all the records for *Puccinellia distans* were either near the coast or part of near-continuous distributions which lead to the coast. A few of the new records reported here are more isolated, but this is probably because the records were single observations sent to the author and the areas around the sites have not yet been revisited. The roadside records of other maritime species are also mostly either confined to sites near the coast or to those which are part of near-continuous populations leading to the coast (Fig. 2). The record for *Armeria maritima* on the A40 near Oxford is an exception to this but as this species is common in gardens this may have been the source of seed in this case. Both of these distribution maps tend to confirm the conclusion, therefore, that these species are originating from local coastal sites. The exclusion of *Puccinellia fasciculata*, a species of southern England, from the list of species present on the roadsides of north-eastern England, removes the one piece of evidence that would suggest some other source.

ACKNOWLEDGMENTS

The author wishes to thank all those who have helped in the publication of this report by contributing records, and the Biological Records Centre at Monks Wood for supplying the base maps. This work forms part of a project funded by a grant from the Natural Environment Research Council.

REFERENCES

Burton, R. M. (1983). Botanical records for 1982. *Lond. Nat.*, **62**: 105–110.

Daniels, E. T. (1984). A Norfolk road verge. *Trans. Norfolk Norwich Nat. Soc.*, **26**: 298–301.

Halliday, G. (1983). Field meetings, 1981: Alston, Cumberland. 12th–13th July. *Watsonia*, **14**: 304.

Hyde, E. M., Hyde, M. A. & Simpson, F. W. (1981). Some recent Suffolk plant records. *Trans. Suffolk Nat. Soc.*, **18**: 232–241.

Hyde, E. M., Hyde, M. A. & Simpson, F. W. (1982). Some recent Suffolk plant records. *Trans. Suffolk Nat. Soc.*, **18**: 298–303.

Hyde, E. M., Hyde, M. A. & Simpson, F. W. (1983). Some recent Suffolk plant records. *Trans. Suffolk Nat. Soc.*, **19**: 362–370.

Kitchener, G. (1983). Maritime plants on inland roads of West Kent. *Trans. Kent Fld Club*, **9**: 87–94.

Mathews, P. & Davison, A. W. (1976). Maritime species on roadside verges. *Watsonia*, **11**: 164.

Phillips, R. (1981). *Mushrooms and other fungi of Great Britain and Europe*. London.

Scott, N. E. (in press). The distribution and ecology of coastal species on roadsides, in *Towards a synthesis of vegetation science, population dynamics and ecophysiology in coastal vegetation*. Yerseke, The Netherlands.

Scott, N. E. & Davison, A. W. (1982). De-icing salt and the invasion of road verges by maritime plants. *Watsonia*, **14**: 41–52.

Thompson, J. R., Rutter, A. J., Ridout, P. S. & Glover, M. (1979). The implications of the use of de-icing salt for motorway planting in the U.K., in Colwel, D. M., Thompson, J. R. & Rutter, A. J., eds. *The impact of road traffic on plants*, pp. 83–90. Transport and Road Research Laboratory supplementary report 513, Crowthorne.

(*Accepted July 1984*)

Watsonia, **15**, 387–389 (1985)

Short Notes

A NEW BRAMBLE FROM HAMPSHIRE

Since the 1870s *Rubus* specialists have been perplexed by a low-growing, glandular bramble with small, narrow, white petals and typically very long panicle branches which is abundant in parts of S. Hants., v.c. 11, chiefly in the fragments of the one-time Forest of Bere Portchester. It was first collected in 1872 by F. Townsend from around his home at Shedfield (**K**) and queried by Babington as *R. drejeri* G. Jensen and then, some years later, referred by Rogers to *R. babingtonii* T. B. Salter (*R. ochrodermis* A. Ley). In 1879 Babington was sent a further gathering of it by J. Groves from north of Southampton (**CGE**), and this time determined it as *R. infestus* Weihe ex Boenn. In 1883 Rogers collected it himself, also near Southampton (**BM**), and had his determination of *R. koehleri* Weihe & Nees confirmed by Focke. In 1902–7 the Rev. W. L. W. Eyre included a series of examples in the collections he submitted to Rogers from the Ellisfield district, south of Basingstoke, in v.c. 12 (**BM**, **HME**), and variously received back as its name *R. uncinatus* P. J. Muell. forma and *R. acutifrons* A. Ley (Eyre 1905). Superficially it does indeed closely resemble the latter, a species of the Welsh Marches, and it was doubtless the plant collected on Southampton Common in 1905 by J. F. Rayner (Rayner 1929) and also determined as that by Rogers. Doubtless too, it was the Southampton Common bramble seen by W. C. R. Watson and J. E. Woodhead in 1951 and queried in the latter's field diary (now in **SLBI**) as *R. pascuorum* Wats. and *R. lintonii* Focke ex Bab. in turn.

Had the successive national specialists only had the opportunity of more than a solitary acquaintance with the plant in the field, this history of confusion would surely not have occurred, for it is exceptionally distinctive and, once known, unlikely to be confounded with any other Wessex species.

Away from its headquarters north and east of Southampton it is found over a wide area of the county, though only very sparsely. Across the New Forest it trickles as far west as Wootton Coppice Inclosure and as far north as Nomansland – where it grows within metres of S. Wilts., v.c. 8. In N. Hants., v.c. 12, in addition to Eyre's Ellisfield district, I have seen it on Hook Common (albeit there as an apparent roost casual) and it has twice been collected by others on Bramshott Common, close to the border with Surrey, v.c. 17. Similarly it occurs close to the border with W. Sussex, v.c. 13, in Havant Forest. There are also two large populations in the Isle of Wight, v.c. 10, in Apse Heath Copse and on Head Down, near Niton.

In common with A. Newton and the late B. A. Miles I have seen no material of this bramble from outside Hampshire and Wight. Accordingly, in view of the fact that it occurs in three vice- counties and continues into three further ones in all probability as well, it now seems overdue for naming.

Rubus hantonensis D. E. Allen, **sp. nov.**

Turio arcuatus obtuse angulatus superficiebus planis vel leviter excavatis purpurascens glabrescens glandulis stipitatis longis et aciculis sparsim et aculeolis brevibus copiose et aculeis ad angulos dispositis gracilibus e basi lata compressa declinatis vel falcatis munitus. Folia quinata digitata latere undulata; foliola non contigua superne fere glabra inferne copiose capillis brevibus pilosa; foliolum terminale 5·0–7·5×3·5–6·0 cm, rotundum vel ovale vel subquadratum vel obovatum acuminatum basi integrum subaequaliter et tenuissime biserratum; petiolus foliolis infimis longior aculeis falcatis munitus. Ramus florifer parum flexuosus purpureus copiose pilosus aciculis glandulisque stipitatis inaequalibus numerosis, aculeis parvis declinatis vel curvatis munitus; inflorescentia pyramidata foliolis cuneatis inferne ramulis axillaribus distantibus saepe longissimis adscendentibus vel divaricatis aucta. Flores c.1·5–2·0 cm in diametro; sepala griseo-viridia anguste albo-marginata satis pilis et glandulis patentibus et reflexis tandem longissimis patentibus appendiculatis; petala lactea anguste obovata vel oblanceolata integra ad marginem glabra distantia; stamina alba stylos pallidos vix superantia; carpella glabra; receptaculum glabrum vel pilosum; fructus parvus rotundus glaucescens.

Stem low-arching, not pruinose, bluntly angled with flat or slightly furrowed sides, dull purple, glabrescent with sparse, patent, chiefly simple hairs, scattered long-stalked glands, rather few acicles and numerous short, occasionally gland-tipped pricklets; prickles confined to the angles, unequal, the longest equalling the stem diameter, contracted suddenly from a broad compressed base, straight or curved, declining to falcate, reddish-purple with yellow point. Leaves digitate; leaflets (3)5, well spaced, glabrescent above, soft beneath with numerous short simple and tufted hairs; terminal leaflet 5–0–7·5×3·5–6·0 cm, round or oval or subquadrate or obovate, with a gradually acuminate apex 1·0–1·5 cm and entire base, finely and more or less evenly biserrate, margin undulate, the petiolule ½–⅔ as long as the lamina; petiole much longer than the basal leaflets with numerous simple and tufted hairs, sparse stalked glands and acicles and small retrorse-falcate prickles. Flowering branch with 3-foliate leaves below and 1–2 simple leaves above, their terminal leaflets cuneate at base; inflorescence pyramidal, interrupted below, with long ascending to divaricate many-flowered lower axillary peduncles, the lowest sometimes subequalling the main axis; rachis slightly flexuose, furrowed, dark purple, with numerous longish simple and tufted hairs, numerous very short, short and long stalked glands, fewer short to medium acicles and numerous small deflexed to retrorse-falcate prickles. Flowers c.1·5–2·0 cm in diameter; sepals greyish-green, narrowly white-bordered, with numerous short and a few long simple and tufted hairs and frequent to numerous very short and medium stalked glands, mixed patent and reflexed, points ultimately very long, patent and appendiculate; petals creamy white, narrowly obovate to oblanceolate, entire, glabrous on the margin, distant; stamens slightly exceeding styles, filaments white, anthers yellow, glabrous; styles pale yellow or pale green; young carpels glabrous; receptacle glabrous or pilose; fruit small, globose, glaucescent.

HOLOTYPUS: Long Aldermoor nature reserve, near Minstead, GR 41/273.097, S. Hants., v.c. 11, 18/7/1984, *D. E. Allen & A. Brewis* (**BM**).

R. hantonensis is best placed in the series *Apiculati* Focke. It can be told at once by its low stature, very long lower panicle branches, cuneate panicle leaflets, finely toothed and disproportionately long-acuminate stem leaflets and small, distant, narrow, white petals. It is characteristic of oak-holly woodland on dry, gravelly soils in light shade.

REFERENCES

Eyre, W. L. W. (1905). Some Hampshire brambles. *Proc. Hants. Fld Club & Arch. Soc.*, **4**: 253–255.
Rayner, J. F. (1929). *A supplement to Frederick Townsend's Flora of Hampshire and the Isle of Wight*, p. 39. Southampton.
Watson, W. C. R. (1958). *Handbook of the Rubi of Great Britain and Ireland*, p. 177. Cambridge.

D. E. Allen
Lesney Cottage, Middle Road, Winchester, Hants., SO22 5EJ

SPERGULA MORISONII BOREAU, A WEED NEW TO IRELAND

Four species of the Caryophyllaceae have been members of the weed flora of arable crops on the peatland experimental farm at Derrybrennan, near Lullymore (v.c. H 19) for a number of years. An Foras Talúntais commenced vegetable crop trials there on a few hectares in 1957 and gradually extended the area cultivated to almost 100 ha as the 1960s advanced. *Sagina procumbens* L., *Stellaria media* L. and *Cerastium fontanum* Baumg. were three of twelve weed species recorded there in 1969 and *Spergula arvensis* L. first was noticed in 1980. The first three are evident in the pre-cultivation stage when milled-over areas are left idle for a number of years, as is *Stellaria alsine* Grimm, which spreads to the milled area from undisturbed bog, but the latter species does not continue into the tillage stage.

A further member of the Caryophyllaceae was observed on the farm in August 1983 and at intervals throughout the winter and spring of 1984. At first it was thought to be a variant of

Spergularia marina (L.) Griseb., but detailed examination has shown it to be *Spergula morisonii* Boreau, which occurs in central Europe, extending southwards to the Iberian peninsula and northern Italy, northwards to central Sweden and, since 1943, westwards to Sussex. It is especially abundant (c. 10–20 plants per m^2) on part of an area which carried an experimental blueberry crop in the twelve-year period 1969–1981, but it occurs elsewhere on the farm and occasional seedlings have grown during the winter from soil samples collected from the farm and set out in a heated greenhouse in seedbank studies. The blueberries included European and American cultivars and all were propagated at the Heermann nurseries at Hanover. It is probable that *Spergula morisonii* arrived from Hanover with the blueberry plants.

The Derrybrennan plants conform to the descriptions of *S. morisonii* given by Garcke (1922) and by Ratter (1964). Voucher specimens have been deposited in **DBN** and in the herbarium of the Agricultural Botany Department of University College, Dublin. The plants are glabrous and occur singly or in colonies, in association (in winter 1984) with *Rumex acetosella* L., *Sagina procumbens*, *Senecio vulgaris* L., *Poa annua* L., *Cardamine hirsuta* L., and *Stellaria media*. Plants in February, March and April were 5 to 15 cm high (generally 6 to 10 cm) possessing a shallow, slender tap-root and a shoot system which branches from the base giving three or four slightly straggling stems, each having three or four internodes and terminating in a small cyme of three to ten flowers, each with usually ten stamens and a whorl of ovate, obtuse, sometimes contiguous petals which equal the sepals in length. The subulate leaves are about 2 cm long. The seeds are distinctly different from those of *Spergularia* and from those of *Spergula arvensis*, and different, but to a lesser degree, from the somewhat larger seeds of the closely related *Spergula pentandra* L., which is reputed to have been collected in Ireland by Sherrard (Babington 1867).

As the seeds are a very distinctive feature of *S. morisonii* they are described here in some detail. To the unaided eye each seed is disc-shaped and has a dull black, or dark brown, circular centre about 0·75 mm in diameter, surrounded by a white translucent wing about 0·25 mm wide. Under magnification, the wing forms a slightly convex or concave circular channel around the seed. The wing has one notch about 0·15 mm deep with a rounded base and with rounded shoulders which are about 0·15 mm apart; occasionally the notch is wider with a tongue projecting to mid-way from its base. The wing has numerous (c. 30 per mm) radial striations and is brown on its inner part, bordering the black or dark brown centre of the seed; the radial striations also are brown on their inner parts but the brown colour fades gradually so that their outer third is without colour; the thinner tissue between the striations appears to be pitted or to have one row of minute brown dots between pairs of striae; the area surrounding the notch is brown, especially around the base; the black centre is raised, sometimes slightly contoured or cratered, and has two to four irregular rows of spaced, white, glandular hairs all around its outer, 0·1 mm wide rim. When imbibed, the dark centre becomes slightly comma-shaped, with its 'tail' extended to the base of the notch. About 25 to 35 seeds are produced per capsule.

REFERENCES

Babington, C. C. (1867). *Manual of British botany*, 6th ed, p. 63. London.
Garcke, A. (1922). *Flora von Deutschland*. Berlin.
Ratter, J. A. (1964). *Spergula*, in Tutin, T. G. *et al.*, eds. *Flora Europaea* **1**: 154. Cambridge.

P. L. Curran & F. S. MacNaeidhe
Agricultural Botany Department, University College, Dublin 4, Ireland

Plant Records

Records for publication must be submitted in the form shown below to the appropriate vice-county Recorder (see list of *County Recorders* (1982)), and *not* the Editors. The records must normally be of species, hybrids or subspecies of native or naturalized alien plants belonging to one or more of the following categories: 1st or 2nd v.c. record, 1st post-1930 v.c. record; only extant v.c. record, or 2nd such record; a record of an extension of range by more than 100 km. Such records will also be accepted for the major islands in v.c. 102–104 and 110. Only 1st records can be accepted for *Rubus*, *Hieracium* and hybrids. Records for subdivisions of vice-counties will not be treated separately; they must therefore be records for the vice-county as a whole. Records of *Taraxacum* are now being dealt with separately, by Dr A. J. Richards, and will be published at a later date.

Records are arranged in the order given in the *List of British vascular plants* by J. E. Dandy (1958) and his subsequent revision (*Watsonia*, **7**: 157–178 (1969)). All records are field records unless otherwise stated. With the exception of collectors' initials, herbarium abbreviations are those used in *British and Irish herbaria* by D. H. Kent & D. E. Allen (1984).

The following signs are used:

* before the record: to indicate a new vice-county record.
† before the species number: to indicate that the plant is not a native species of the British Isles.
† before the record: to indicate a species which, though native in some parts of the British Isles, is not so in the locality recorded.
[] enclosing a previously published record: to indicate that the record should be deleted.

1/2. LYCOPODIELLA INUNDATA (L.) Holub **107**, E. Sutherland: Crask Inn, Loch Gaineamach, GR 29/51.25. Peat bog. E. Charter, 1984, **E.** 2nd record.

†12/1. ONOCLEA SENSIBILIS L. *__73__, Kirkcudbrights.: Island below Creebridge, Minnigall, GR 25/41.65. Shingle. H. Lang, 1980, **E.**

†17/1. MATTEUCCIA STRUTHIOPTERIS (L.) Tod. *__73__, Kirkcudbrights.: Shambellie, New Abbey, GR 25/95.66. O. M. Stewart, 1980. Southwick Burn near Southwick House, GR 25/93.57. Wood. O. M. Stewart, 1982. 1st and 2nd records.

21/2 bor. DRYOPTERIS AFFINIS (Lowe) Fraser-Jenkins subsp. BORRERI (Newman) Fraser-Jenkins *__83__, Midlothian: Linn Dean below Soutra Hill, GR 36/46.59. Rocky bank. B.P.S./B.S.E. meeting, 1984, det. C. N. Page.

21/2 rob. DRYOPTERIS AFFINIS (Lowe) Fraser-Jenkins subsp. ROBUSTA Oberholzer & von Tavel ex Fraser-Jenkins *__83__, Midlothian: Linn Dean below Soutra Hill, GR 36/46.59. Rocky bank. B.P.S./B.S.E. meeting, 1984, det. C. N. Page.

21/2 sti. DRYOPTERIS AFFINIS (Lowe) Fraser-Jenkins subsp. STILLUPENSIS (Sabransky) Fraser-Jenkins *__49__, Caerns.: Near Betws Garmon, GR 23/54.56. Rock scree. R. H. Roberts, 1979, **herb. R.H.R.**, det. C. R. Fraser-Jenkins.

21/3. DRYOPTERIS OREADES Fomin **46**, Cards.: Rhuddnant gorge, GR 22/80.78. Rock crevices. W. M. Condry, A. O. Chater & D. G. Jones, 1984, **NMW**. 2nd record.

21/7×6. DRYOPTERIS DILATATA (Hoffm.) A. Gray×D. CARTHUSIANA (Vill.) H. P. Fuchs *__84__, W. Lothian: Bathgate, GR 36/00.70. Hedgerow. F. A. & E. M. Kirk, 1983, **E**, det. J. Ratter & D. R. McKean.

21/8. DRYOPTERIS AEMULA (Ait.) Kuntze **44**, Carms.: Amroth valley, GR 22/17.07. Rock outcrop. E. J. Hannah, 1983, **NMW**, det. I. K. Morgan. 2nd extant record.

22/2×1. POLYSTICHUM ACULEATUM (L.) Roth×P. SETIFERUM (Forsk.) Woynar *__72__, Dumfriess.: Rockhall Burn, Collin, GR 35/05.75. Shaded ravine. H. Milne-Redhead, 1973, **K**, det. B. S. Croxall. *__80__, Roxburghs.: Greypeel Burn, GR 36/64.17. Wooded ravine. R. W. M. Corner, 1983, **BM**, conf. J. Camus.

25/int.×1. POLYPODIUM INTERJECTUM Shivas×P. VULGARE L. ***38**, Warks.: Rugby, GR 42/50.74. Brick wall. R. P. H. Lamb, 1983, **WAR**, det. R. H. Roberts.

26/1. PILULARIA GLOBULIFERA L. **107**, E. Sutherland: R. Oykel 10 km SW. of Lairg, GR 29/48.00. E. Charter, 1984, **E**. 1st record since 1893.

†27/1. AZOLLA FILICULOIDES Lam. ***45**, Pembs.: R. Alun, St David's, GR 12/75.25. Running water. G.C. Lambourne, 1984. ***85**, Fife: Leslie, GR 37/26.01. Small pond. T. Gray, 1984.

46/5. RANUNCULUS ARVENSIS L. **50**, Denbs.: Pentre Broughton, GR 33/30.52. Waste ground. H. Noltie, 1984. 2nd record.

46/9. RANUNCULUS PARVIFLORUS L. **38**, Warks.: Hampton Lucy, GR 42/25.59. Scrub. J. C. Bowra, 1983, **WAR**. 2nd record.

46/11. RANUNCULUS LINGUA L. ***44**, Carms.: Witchett Pool, Laugharne, GR 22/28.07. Marginal fen. I. Smith & A. Burn, 1984, **NMW**. 1st record of a native population.

46/16. RANUNCULUS HEDERACEUS L. **103**, Mid Ebudes: An Fhaodail, Tiree, GR 17/01.44. Wet muddy hollow. P. Wormell, 1983. 1st Tiree record.

46/20. RANUNCULUS CIRCINATUS Sibth. **68**, Cheviot: R. Bowmont near Mindrummill, GR 36/85.33. Backwater pond. G. A. & M. Swan, 1984, **herb. G.A.S.** 1st post-1930 record.

46/22b. RANUNCULUS PELTATUS Schrank ***77**, Lanarks.: Cowgill, GR 36/00.29. Reservoir. R. C. L. Howitt, 1979. Wolfclyde, Biggar, GR 36/01.36. River. P. Macpherson, 1980, conf. N.T.H. Holmes. Both **herb. P. M.** 1st and 2nd records.

46/23. RANUNCULUS BAUDOTII Godr. ***94**, Banffs.: Tugnet, Spey Bay, GR 38/34.65. Ditch. M. McC. Webster, 1983, **E**.

48/1. MYOSURUS MINIMUS L. **12**, N. Hants.: Freelands Farm, Church Crookham, GR 41/80.52. S. & J. Ash, 1983. 2nd extant record.

50/1. THALICTRUM FLAVUM L. **50**, Denbs.: Rosset, GR 33/3.5. Hedge bank. J. A. Green, 1984. 2nd extant record.

58/3. PAPAVER LECOQII Lamotte **45**, Pembs.: Solva, GR 12/79.24. Roadside. Q. Kay, 1984. 2nd record.

66/2. FUMARIA CAPREOLATA L. **67**, S. Northumb.: Newton Hall, GR 45/03.65. Roadside bank. G. A. Swan, 1984, **herb. G.A.S.** 1st record since 1867.

66/6b. FUMARIA MURALIS Sond. ex Koch subsp. BORAEI (Jord.) Pugsl. ***107**, E. Sutherland: Newton Point, GR 28/71.87. Cultivated field. J. K. Butler, 1984, **E**.

†67/2. BRASSICA NAPUS L. ***94**, Banffs.: Tomintoul, GR 38/16.19. Waste ground. Tugnet, Spey Bay, GR 38/34.65. River shingle. Both M. McC. Webster, 1983. 1st and 2nd records. **103**, Mid Ebudes: Cliad, Coll, GR 17/20.59. Field edges. J. W. Clark, 1984, **E**. 1st Coll record.

†67/elo. BRASSICA ELONGATA Ehrh. **69**, Westmorland: Ulverston, GR 34/30.77. G. Halliday, 1984, **LANC**, conf. E. J. Clement. 1st post-1930 record.

†68/1. ERUCASTRUM GALLICUM (Willd.) O. E. Schulz ***70**, Cumberland: R. Eden S of Kirkoswald, GR 35/55.40. Disturbed ground. R. E. Groom, 1984, **LANC**, det. G. Halliday.

69/1. RHYNCHOSINAPIS MONENSIS (L.) Dandy: †***77**, Lanarks.: Hyndland, Glasgow, GR 26/55.67. Waste ground. A. McG. Stirling, 1983, **herb. P. Macpherson**.

†72/1. DIPLOTAXIS MURALIS (L.) DC. **77**, Lanarks.: Carmyle, Glasgow, GR 26/6.6. J. H. Penson, 1958, **herb. J. H. P.** , conf. A. McG. Stirling. 2nd record.

79/6. LEPIDIUM LATIFOLIUM L. **44**, Carms.: Pant-yr-athro, Llansteffan, GR. 22/36.12. Upper saltmarsh. I. K. Morgan, 1984, **NMW**, conf. R. G. Ellis. 2nd record.

†79/7. LEPIDIUM GRAMINIFOLIUM L. **59**, S. Lancs.: Queens Park, Bolton, GR 34/70.09. J. Percy, 1984. 2nd record.

†80/2. Coronopus didymus (L.) Sm. ***101**, Kintyre: Between Torrisdale and Saddell, GR 16/79.33. Strand line on shore. A. G. Kenneth, 1984, **herb. A.G.K.**

†83/umb. Iberis umbellata L. ***44**, Carms.: Ystradowen, GR 22/75.12. Waste ground. G. Hutchinson, 1982. Pantyffynnon, GR 22/62.10. River-bank. A. M. Pell, 1984. Both **NMW**, conf. R. G. Ellis. 1st and 2nd records.

84/1. Thlaspi arvense L. **99**, Dunbarton: Duntocher, Glasgow, GR 26/4.7. Garden weed. A. McG. Stirling, 1984, **E**. 1st post-1930 record.

†100/3. Arabis caucasica Willd. ***69**, Westmorland: Levens, GR 34/48.86. Limestone quarry. M. Andrews, 1984, **LANC**. ***77**, Lanarks.: Crossford, GR 26/82.47. River bank. P. & E. L. S. Macpherson, 1979, **herb. P.M.**, det. E. J. Clement.

†Lunaria annua L. ***94**, Banffs.: Ballindalloch, GR 38/17.37. M. McC. Webster, 1983.

102/1. Rorippa nasturtium-aquaticum (L.) Hayek ***80**, Roxburghs.: Burnfoot, Hawick, GR 36/52.16. Edge of R. Teviot. R. W. M. Corner, 1984, **herb. R.W.M.C.**

102/2. Rorippa microphylla (Boenn.) Hyland. ***44**, Carms.: Penrhiwgoch, GR 22/55.18. Wet pasture. A. M. Pell, 1983, **NMW**, conf. R. G. Ellis.

†105/1. Erysimum cheiranthoides L. ***73**, Kirkcudbrights.: Sandy Hills, GR 25/89.55. O. M. Stewart, 1984, **E**.

†111/1. Descurainia sophia (L.) Webb ex Prantl **35**, Mons.: Chepstow, GR 31/52.93. Garden weed. T. G. Evans, 1984, **herb. T.G.E.** 2nd extant record.

113/6. Viola canina L. ***79**, Selkirks.: R. Yarrow, Bowhill, GR 36/42.28. Rocks by river. 1983. ***80**, Roxburghs.: R. Tweed, Trows, Makerstoun, GR 36/68.32. Rocks by river. 1984. Both R. W. M. Corner, **herb. R.W.M.C.**, conf. D. H. Valentine.

115/1. Hypericum androsaemum L. **80**, Roxburghs.: R. Teviot above Hornshole Bridge, GR 36/53.16. Rock ledge. R. W. M. Corner, 1984. 1st post-1930 record.

115/6a. Hypericum maculatum Crantz subsp. maculatum **103**, Mid Ebudes: Glenforsa Lodge, Mull, GR 17/59.42. Roadside. A. McG. Stirling, 1984, **BM**, conf. N. K. B. Robson. 1st record since 1889.

115/6×5. Hypericum maculatum Crantz×H. perforatum L. ***72**, Dumfriess.: 2 miles E. of Moniaive, GR 25/79.89. Roadside verge. J. K. Butler, 1980, det. N. K. B. Robson. 1st confirmed record.

127/1. Dianthus armeria L. **12**, N. Hants.: Whitehill, Woolmer Forest, GR 41/79.33. Fire-break. C. Moss, 1984, **herb. A. Brewis**. 2nd record.

130/nan. Petrorhagia nanteuilii (Burnat) P. W. Ball & Heywood †***35**, Mons.: Chepstow, GR 31/52.93. Garden weed. T. G. Evans, 1984, **herb. T.G.E.**

131/2×†3. Cerastium arvense L.×C. tomentosum L. ***29**, Cambs.: Between Chippenham and Freckenham, GR 52/66.71. Roadside. A. C. Leslie, 1979, **CGE**. ***83**, Midlothian: Borthwick Bank, GR 36/37.60. Railway embankment. O. M. Stewart, 1983, **E**, conf. A. C. Leslie.

131/10. Cerastium diffusum Pers. ***43**, Rads.: N. of Llanerch-y-cawr, GR 22/90.61. R. G. Woods, 1984, **NMW**.

†131/bie. Cerastium biebersteinii DC. ***94**, Banffs.: Gamrie, GR 38/80.64. Roadside verge. M. McC. Webster, 1983, **E**.

132/1. Myosoton aquaticum (L.) Moench †***68**, Cheviot: R. Tweed near Carham Hall, GR 36/80.39. River gravels. G. A. & M. Swan, 1984.

133/3. Stellaria pallida (Dumort.) Piré ***83**, Midlothian: Colinton Dell, Edinburgh, GR 36/21.69. Cut grass. O. M. Stewart, 1984, **E**. **94**, Banffs.: Buckpool, GR 38/40.64. Sandy ground. M. McC. Webster, 1983. 2nd record.

136/3. Sagina maritima Don **29**, Cambs.: Foul Anchor, GR 53/46.17. Strand line by river. A. C. Leslie, 1983, **CGE**. First post-1930 record.

137/4. Minuartia hybrida (Vill.) Schischk. †***48**, Merioneth: 1 km NE. of Llangower, GR 23/91.33. Railway ballast and adjacent rocks. P. M. Benoit, E. D. Pugh & M. Wainwright, 1983, **NMW**.

†141/6. Arenaria balearica L. ***44**, Carms.: Dynevor Deer Park, Llandeilo, GR 22/61.22. Wall. R. G. Woods, 1984.

143/5. Spergularia marina (L.) Griseb. **94**, Banffs.: Tugnet, Spey Bay, GR 38/34.65. Maritime shingle. M. McC. Webster, 1983. 1st post-1930 record.

149/1b. Montia fontana L. subsp. chondrosperma (Fenzl) Walters ***94**, Banffs.: Blacksboat, GR 38/17.37. River shingle. R. Fitzgerald, 1983, det. A. J. Silverside.

†149/2. Montia perfoliata (Willd.) Howell ***103**, Mid Ebudes: Rubha nan Gall, Mull, GR 17/50.56. A. Wright, 1984.

†151/1. Portulaca oleracea L. ***70**, Cumberland: Folly Lane, Penrith, GR 35/51.30. Garden weed. V. Burbury, 1984, **LANC**.

†153/1. Amaranthus retroflexus L. ***70**, Cumberland: R. Eden S. of Kirkoswald, GR 35/55.40. Disturbed ground. R. E. Groom, 1984, **LANC**, det. G. Halliday.

154/14. Chenopodium rubrum L. ***50**, Denbs.: Pantyrochain near Gresford, GR 33/34.53. Dried-up pool. J. B. Formstone, 1984, **NMW**, conf. R. G. Ellis.

†154/16. Chenopodium glaucum L. ***85**, Fife: Earlshall, GR 37/49.22. Shore. S. J. Leach, 1979.

156/5. Atriplex laciniata L. **4**, N. Devon: Instow, GR 21/47.31. Sandy shore. M. Tulloh, 1965. 1st post-1930 record.

156/lon. Atriplex longipes Drejer **73**, Kirkcudbrights.: Nether Clifton, GR 25/91.56. Merse land. O. M. Stewart, 1984, **E**. 2nd record.

156/pra. Atriplex praecox Hülphers ***101**, Kintyre: S. of Kilmory, GR 16/71.83. Shingle. A. G. Kenneth, 1984, **herb. P. Taschereau**, det. P.T.

160/2. Salicornia dolichostachya Moss ***67**, S. Northumb.: Amble, GR 46/26.05. Saltmarsh. ***68**, Cheviot: Lowmoor Point, GR 46/09.39. Saltmarsh. Alnmouth, GR 46/24.10. Saltmarsh. 1st and 2nd records. All G. A. & M. Swan, 1962, det. P. W. Ball & T. G. Tutin.

160/4. Salicornia ramosissima Woods ***68**, Cheviot: Holy Island, GR 46/09.43. Saltmarsh. G. A. & M. Swan, 1983, det. D. H. Dalby. Long Nanny, GR 46/22.27. Saltmarsh. G. A. Swan, 1984, det. I. K. Ferguson. 1st and 2nd authenticated records.

160/5. Salicornia pusilla Woods **44**, Carms.: Pembrey Burrows, GR 21/41.99. Upper saltmarsh. R. D. Pryce, 1984, **K**, det. I. K. Ferguson. 2nd record.

160/fra. Salicornia fragilis P. W. Ball & Tutin (including *S. lutescens* P. W. Ball & Tutin) ***67**, S. Northumb.: R. Blyth, GR 45/29.82. Upper saltmarsh. G. A. Swan, 1984, det. I. K. Ferguson. ***68**, Cheviot: Beal, GR 46/08.42. Saltmarsh. G. A. & M. Swan, 1962, det. P. W. Ball & T. G. Tutin. Alnmouth, GR 46/24.09. Saltmarsh. G. A. Swan, 1984, det. I. K. Ferguson. 1st and 2nd records.

†168/3×4. Geranium endressii Gay×G. versicolor L. ***44**, Carms.: The Plas, Llansteffan, GR 22/34.10. Pasture. H. Sealy-Lewis, 1984, **NMW**, det. R. G. Ellis & T. G. Evans.

168/7. Geranium sanguineum L. ***107**, E. Sutherland: The Mound, Golspie, GR 28/78.98. Rocky scrub. C. Lawson, 1983.

†168/ibi.×pla. Geranium ibiricum Cav.×G. platypetalum Fischer & C. A. Meyer ***77**, Lanarks.: Cuningar Loop, Glasgow, GR 26/62.63. Waste ground. A. McG. Stirling & A. J. Silverside, 1981.

169/2. ERODIUM MOSCHATUM (L.) L'Hérit. †**38**, Warks.: Leamington Spa, GR 42/32.65. M. J. Senior, 1984, det. J. C. Bowra. 1st record since 1884.

†171/2. IMPATIENS CAPENSIS Meerb. **35**, Mons.: Tredegar Park, Newport, GR 31/28.85. J. P. Curtis, 1984. Only extant record.

178/1. BUXUS SEMPERVIRENS L. †***103**, Mid Ebudes: Garmony, Mull, GR 17/67.40. J. W. Clark, 1981, **BM**.

†181/1. VITIS VINIFERA L. ***44**, Carms.: Capel Hendre, GR 22/59.11. A. M. Pell, 1983, **NMW**. Pembrey Forest, GR 22/39.01. Llanelli Naturalists, 1984, det. I. K. Morgan & R. D. Pryce. 1st and 2nd records.

†183/2×pol. LUPINUS ARBOREUS Sims×L. POLYPHYLLUS Lindley ***77**, Lanarks.: Cuningar Loop, Glasgow, GR 26/62.62. P. & A. C. Macpherson, 1981, **herb. P.M.**, det. A. J. Silverside.

†183/pol. LUPINUS POLYPHYLLUS Lindley ***94**, Banffs.: Nether Dallacy, GR 38/36.64. Gravel pit. M. McC. Webster, 1980.

185/2. GENISTA ANGLICA L. **59**, S. Lancs.: Highfield Moss, GR 33/61.95. Dry heath. P. Jepson, 1984. First post-1930 record.

190/4. MEDICAGO MINIMA (L.) Bartal. †**38**, Warks.: Saltisford, Warwick, GR 42/27.65. V. & J. R. Roberts, 1972, det. C. C. Townsend. 2nd record.

190/5. MEDICAGO POLYMORPHA L. †**38**, Warks.: Warwick, GR 42/27.65. V. & J. R. Roberts, 1981, det. C. C. Townsend. 2nd record.

†191/4. MELILOTUS INDICA (L.) All. ***99**, Dunbarton: Strathleven, Dumbarton, GR 26/39.77. Waste ground. A. McG. Stirling & A. Rutherford, 1984, **E**.

†192/22. TRIFOLIUM AUREUM Poll. ***77**, Lanarks.: Hyndland, Glasgow, GR 26/55.67. A. McG. Stirling, 1983, **herb. P. Macpherson**.

206/10. VICIA SYLVATICA L. **52**, Anglesey: Porth-y-gwichiaid, Llaneilian, GR 23/48.91. Sea cliff. P. Day, 1984. 1st post-1930 record.

207/2. LATHYRUS NISSOLIA L. ***4**, N. Devon: Instow, GR 21/47.29. Railway cutting. M. Tulloh, 1976.

207/6. LATHYRUS SYLVESTRIS L. **81**, Berwicks.: Cripplenick, Edington Mains, GR 36/90.54. Sandstone crag. M. E. Braithwaite, 1984, **herb. M.E.B.** 1st post-1930 record.

†207/8. LATHYRUS LATIFOLIUS L. ***77**, Lanarks.: Meadowside, GR 26/55.66. Disused railway track. P. Macpherson & A. McG. Stirling, 1983, **herb. P.M.**

†207/gra. LATHYRUS GRANDIFLORUS Sibth. & Sm. ***44**, Carms.: Pembrey, GR 22/43.01. Hedge. F. H. Webb, 1984, **NMW**.

†208/1. PHYSOCARPUS OPULIFOLIUS (L.) Maxim. ***77**, Lanarks.: Bishop Loch, Glasgow, GR 26/68.66. P. Macpherson & A. G. Carstairs, 1981, **herb. P.M.**, det. E. J. Clement.

†209/2×1. SPIRAEA DOUGLASII Hook.×S. SALICIFOLIA L. ***77**, Lanarks.: Carstairs, GR 26/97.47. Hedge bank. A. McG. Stirling, 1981. ***80**, Roxburghs.: Cavers, Hawick, GR 36/54.14. Wood. 1976. R. W. M. Corner, **herb. R.W.M.C.**, det. A. J. Silverside.

†209/alb. SPIRAEA ALBA Duroi ***80**, Roxburghs.: Whitehaugh, GR 35/52.91. Hedge. R. W. M. Corner, 1981, **herb. R.W.M.C.**, det. A. J. Silverside.

†209/alb.×1. SPIRAEA ALBA Duroi×S. SALICIFOLIA L. ***80**, Roxburghs.: NW. of Wolflee, GR 36/57.10. Roadside. 1981. R. W. M. Corner, **herb. R.W.M.C**, det. A. J. Silverside.

†209/alb.×2. SPIRAEA ALBA Duroi×S. DOUGLASII Hook. ***94**, Banffs.: Ballindalloch, GR 38/17.37. M. McC. Webster, 1983, **E**, det. A. J. Silverside.

†210/pur. FILIPENDULA PURPUREA Maxim. ***77**, Lanarks.: Cathkin, GR 26/62.58. Roadside. P. Macpherson & E. L. S. Lindsay, 1983, **herb. P.M.**, det. D. McClintock.

211/9. RUBUS CAESIUS L. **80**, Roxburghs.: Jerdonfield, Monteviot, GR 36/65.23. Roadside verge. R. W. M. Corner, 1983, **herb. R.W.M.C.**, conf. A. Newton. 1st localized record since 1887.

211/11/1. RUBUS NESSENSIS W. Hall *__94__, Banffs.: Kilnmaichlie, Glen Avon, GR 38/18.32. Roadside. M. McC. Webster, 1983, **E**, det. A. Newton.

211/11/2. RUBUS SCISSUS W. C. R. Wats. *__94__, Banffs.: Lyne of Carron, GR 38/22.39. B.S.B.I. Meeting, 1983, **E**, conf. A. Newton.

211/11/99. RUBUS SEPTENTRIONALIS W. C. R. Wats. **103**, Mid Ebudes: Arinagour, Coll, GR 17/2.5. J. W. Clark, 1984, **E**, det. A. McG. Stirling. Druim a'Choirce, Tiree, GR 17/07.48. J. W. Clark, 1984, det. A. Newton. 1st records from Coll and Tiree.

211/11/115. RUBUS RHOMBIFOLIUS Weihe ex Boenn. *__69__, Westmorland: Between Finsthwaite and Graythwaite, GR 34/37.89. Roadside rocks. H. Caldwell, 1984, **LANC**, det. A. Newton.

211/11/284. RUBUS RUFESCENS Muell. & Lefèv. *__103__, Mid Ebudes: Aros Park, Mull, GR 17/51.53. Wood. A. McG. Stirling, 1984, **E**.

211/11/pis. RUBUS PISTORIS Barton & Riddelsd. *__101__, Kintyre: Craiglin, Achnamara, GR 16/77.87. Roadside. A. G. Kenneth, 1984, **herb. A.G.K.**, det. A. Newton.

†212/9. POTENTILLA INTERMEDIA L. *__38__, Warks.: Water Orton, GR 42/16.91. Disused railway sidings. S. O'Donnell, 1981, **herb. E.J. Clement**, det. E.J.C.

212/13 str. POTENTILLA ERECTA (L.) Räusch. subsp. STRICTISSIMA A. J. Richards *__94__, Banffs.: Kilnmaichlie, GR 38/18.33. Moorland. Stobach, GR 38/17.29. Moorland. Both B.S.B.I. Meeting, 1983. 1st and 2nd records.

218/2. AGRIMONIA PROCERA Wallr. *__94__, Banffs.: Arndilly, Craigellachie, GR 38/29.45. R. Fitzgerald, 1983.

†220/3/12. ALCHEMILLA MOLLIS (Buser) Rothm. *__77__, Lanarks.: R. Cart, Linn, Glasgow, GR 26/58.58. River bank. P. Macpherson, 1984, **herb. P.M.**

†220/3/tyt. ALCHEMILLA TYTTHANTHA Juz. *__80__, Roxburghs.: S. side of Ettrick Water, GR 36/48.32. Old track. R. W. M. Corner, 1984, **CGE**, det. S. M. Walters.

†225/5. ROSA RUGOSA Thunb. *__94__, Banffs.: Craigroy, Kilnmaichlie, GR 38/18.34. B.S.B.I. Meeting, 1983.

225/8×13. ROSA CANINA L.×R. MOLLIS Sm. *__17__, Surrey: Ham, GR 51/16.72. Gravel pits. S.F.C. Meeting, 1983, det. R. Melville.

†226/3. PRUNUS CERASIFERA Ehrh. *__35__, Mons.: S. Bargoed Farm, GR 31/46.94. Hedge. Crick, GR 31/48.89. Hedge. Both T. G. Evans, 1984. 1st and 2nd records. *__47__, Monts.: Llansantffraid, GR 33/2.2. E. D. Pugh, 1984, **NMW**.

†227/bul. COTONEASTER BULLATUS Boiss. *__44__, Carms.: Capel Hendre, GR 22/59.11. Hedge. A. M. Pell, 1984, **NMW**, det. R. G. Ellis.

†227/die. COTONEASTER DIELSIANUS E. Pritzel ex Diels *__49__, Caerns.: Edeyrn, GR 23/27.95. Wall top. A. P. Conolly, 1981, **herb. A.P.C.**, det. C. A. Stace.

229/1. CRATAEGUS LAEVIGATA (Poir.) DC. **83**, Midlothian: Arniston Glen, GR 36/32.59. Wood. D. R. McKean, 1980. 2nd record.

†235/3. SEDUM SPURIUM Bieb. *__38__, Warks.: Near Bearley, GR 42/18.60. Roadside. J. C. Bowra, 1984, **WAR**, det. P. J. Copson. *__77__, Lanarks.: Near Renfrew, GR 26/51.67. Old railway track. P. Macpherson & E. Teasdale, 1983, **herb. P.M.**

235/10. SEDUM FORSTERIANUM Sm. †**45**, Pembs.: Camrose, GR 12/92.20. J. Hannah, 1984. 2nd record.

237/2. CRASSULA AQUATICA (L.) Schönl. †*__57__, Derbys.: Clubmill Reservoir, Brockwell, GR 43/37.71. R. Woods & M. C. Hewitt, 1984, **DBY**.

†237/hel. CRASSULA HELMSII (T. Kirk) Cockayne *4, N. Devon: Instow, GR 21/48.29. Pond. M. Tulloh, 1973, **BM**. *41, Glam.: Broad Pool, Gower, GR 21/51.91. Pool. R. S. Cropper, 1984. Millbrook Road, Dinas Powys, GR 31/15.71. Garden pond. J. Kilpatrick, 1984, **NMW**, conf. R. G. Ellis. 1st and 2nd records. *57, Derbys.: Tapton Grove, GR 43/40.72. Pond. M. C. Hewitt, 1984, **DBY**. *59, S. Lancs.: Littleborough, GR 34/9.1. Old brickworks. D. Smith, 1979.

†240/1. TELLIMA GRANDIFLORA (Pursh) Dougl. ex Lindl. **94**, Banffs.: Ballindalloch, GR 38/17.37. M. McC. Webster, 1983. 2nd record.

†246/4. RIBES SANGUINEUM Pursh *77, Lanarks.: East Kilbride, GR 26/66.55. Wooded river bank. P. Macpherson & E. L. S. Lindsay, 1983, **herb. P.M.**

250/1 por. LYTHRUM PORTULA (L.) D. A. Webb subsp. PORTULA **94**, Banffs.: Knock, GR 38/14.27. Old mill pond. B.S.B.I. Meeting, 1983, **E**. 2nd extant record.

251/2. DAPHNE LAUREOLA L. *46, Cards.: Nanternis, GR 22/37.56. Ash wood. A. O. Chater, 1984, **NMW**. 1st record of a native population.

†254/6. EPILOBIUM CILIATUM Rafin. *103, Mid Ebudes: Ulva House, Ulva, GR 17/4.3. Garden. Middleton, Tiree, GR 07/94.42. Shelter belt. Both J. W. Clark, 1982, **E**, det D. R. McKean. 1st Mull and Tiree records.

†254/13. EPILOBIUM BRUNNESCENS (Cockayne) Raven & Englehorn **103**, Mid Ebudes: Arinagour, Coll, GR 17/2.5. Garden path. B. Cassels, 1984, **E**. 1st Coll record.

†256/fal. OENOTHERA FALLAX Renner *73, Kirkcudbrights.: Preston Merse, GR 25/94.55. Sand dunes. O. M. Stewart, 1981, **E**, det. K. Rostański.

†259/aqu. MYRIOPHYLLUM AQUATICUM (Velloso) Verdc. *17, Surrey: Woking, GR 41/97.57. Canal. A. C. Leslie, 1983. Elstead, GR 41/92.43. Dried-up pond. J. F. Leslie, J. E. Smith & A. J. Stevens, 1984. 1st and 2nd records.

276/1. MYRRHIS ODORATA (L.) Scop. †**12**, N. Hants.: Stokehill Farm, GR 41/39.51. G. D. Field, 1983. 2nd record.

285/4. APIUM INUNDATUM (L.) Reichb. f. **72**, Dumfriess.: Upper Loch, Lochmaben, GR 35/07.83. M. E. R. Martin, 1984, **DFSM**. 1st record since 1840.

297/1. BERULA ERECTA (Huds.) Coville **67**, S. Northumb.: R. Pont W. of Ponteland, GR 45/14.72. G. A. Swan, 1984. 1st record since 1805.

300/7. OENANTHE FLUVIATILIS (Bab.) Colem. **38**, Warks.: R. Avon, Rugby, GR 42/50.76. Shallow river. J. W. Lewis, 1984, det. J. C. Bowra. 1st post-1930 record.

304/1. MEUM ATHAMANTICUM Jacq. **85**, Fife: Lothrie Burn, Ballingall, GR 37/24.02. Steep bank. S. J. Leach, 1984. 1st record since 1872.

†307/2. ANGELICA ARCHANGELICA L. *77, Lanarks.: R. Kelvin, Yorkhill, GR 26/55.66. River bank. P. Macpherson, 1984, **herb. P.M.**, conf. T. G. Tutin.

318/2. MERCURIALIS ANNUA L. †*43, Rads.: Llandrindod Wells, GR 32/05.61. Waste ground. A. P. Conolly, 1984.

319/11. EUPHORBIA EXIGUA L. **67**, S. Northumb.: Big Waters, GR 45/22.73. Arable weed. D. G. Long, 1967, **HAMU**. 1st post-1930 record. Near Annitsford, GR 45/26.74. Arable weed. G. A. Swan, 1984, **herb. G.A.S.** 2nd extant record.

†319/15. EUPHORBIA ESULA L. **80**, Roxburghs.: Lowood Bridge, GR 36/52.34. Parapet. R. W. M. Corner, 1983, **herb. R.W.M.C.** 1st localized record since 1926.

†319/15×wal. EUPHORBIA ESULA L.×E. WALDSTEINII (Soják) A. Radcl.-Sm. *38, Warks.: Stockton, GR 42/44.64. Edge of arable field. Mr & Mrs J. R. Roberts, 1983, det. A. Radcliffe-Smith.

320/1/4. Polygonum arenastrum Bor. **94**, Banffs.: Milton, GR 38/14.24. Track. S. & V. Heyward, 1981. 2nd record. ***107**, E. Sutherland: Kilphedir, GR 39/98.18. Roadside verge. J. K. & S. I. Butler & M. Murray, 1984, **E**, det. B. T. Styles.

320/6. Polygonum bistorta L. **52**, Anglesey: Maes-y-Porth, Dwyran, GR 23/45.65. Wood. North Wales Nat's Trust Survey Team, 1984. 1st post-1930 record.

†320/22. Polygonum campanulatum Hook. f. ***59**, S. Lancs.: NE. of Bromley Cross Station, GR 34/73.13. Hedgerow. P. Jepson, 1980.

†Rheum×cultorum Thorsrud & Reisaeter ***82**, E. Lothian: R. Tyne, Tyninghame, GR 36/61.78. Wooded river bank. A. J. Silverside, 1983.

325/1/2. Rumex angiocarpus Murb. ***79**, Selkirks.: Douglas Burn, Craig Douglas, GR 36/29.24. Stabilized shingle. R. W. M. Corner, 1984, **herb. R.W.M.C.**, det. J. R. Akeroyd.

325/1/3. Rumex tenuifolius (Wallr.) Löve ***80**, Roxburghs.: E. of Dinlabyre, GR 35/54.90. Forestry track. R. W. M. Corner, 1984, **herb. R.W.M.C.**, det. J. R. Akeroyd. **94**, Banffs.: N. of Inchrory, GR 38/17.08. River shingle. M. McC. Webster, 1982. 2nd record.

†325/10. Rumex patientia L. ***59**, S. Lancs.: Hamerton Road, Colyhurst, GR 33/85.99. Railway embankment. D. P. Earl, 1983, det. J. R. Akeroyd.

325/11×12. Rumex crispus L.×R. obtusifolius L. ***77**, Lanarks.: South Cathkin, GR 26/62.57. Trackside. P. Macpherson & A. McG. Stirling, 1983.

325/18. Rumex maritimus L. **68**, Cheviot: Pallinsburn, GR 36/89.38. Mud by pond. G. A. & M. Swan, 1972, **herb. G.A.S.**, det. J. E. Lousley. R. Tweed near Carham Hall, GR 36/80.39. Wet bank. G. A. & M. Swan, 1984, **herb. G.A.S.** Only extant records.

326/1. Parietaria judaica L. †***103**, Mid Ebudes: Duart Castle, Mull, GR 17/74.35. Old wall. R. W. M. Corner, 1983.

329/1. Humulus lupulus L. †**94**, Banffs.: Ballindalloch, GR 38/16.36. B.S.B.I. Meeting, 1983. 2nd record.

†331/1. Ficus carica L. ***103**, Mid Ebudes: Tobermory, Mull, GR 17/50.55. Wood. A. Wright, 1984, **E**.

335/3. Betula nana L. **94**, Banffs.: Faindoran, Glen Avon, GR 38/09.06. B.S.B.I. Meeting, 1983, **E**. 1st post-1930 record.

342/2. Populus canescens (Ait.) Sm. †***69**, Westmorland: R. Lyvennet, Crossrigg Hall, Cliburn, GR 35/60.24. R. W. M. Corner, 1984, **LANC**.

343/6×9. Salix purpurea L.×S. viminalis L. ***29**, Cambs.: R. Great Ouse, Littleport, GR 52/57.87. River bank. A. C. Leslie, 1984, **herb. A.C.L.**, det. R. D. Meikle. 1st confirmed record.

343/13×16. Salix aurita L.×S. repens L. ***94**, Banffs.: Cairn Gorm, GR 38/00.00. Rock ledge. D. Batty, 1982, **E**, det. D. R. McKean. ***107**, E. Sutherland: Strathsteven, GR 28/88.01. Seashore. B.S.B.I. Meeting, 1983, **E**, det. R. D. Meikle.

343/17. Salix lapponum L. **94**, Banffs.: Cairn Gorm, GR 38/00.00. Rocks. D. Batty, 1982. 1st post-1930 record.

343/20. Salix myrsinites L. **94**, Banffs.: Faindoran, Glen Avon, GR 38/10.05. Moor. B.S.B.I. Meeting, 1983, **E**. 2nd record.

†352/1. Pernettya mucronata (L.f.) Gaudich. ex Spreng. ***69**, Westmorland: Island W. of Belle Isle, Windermere, GR 34/38.96. Wood. C. D. Pigott, 1970. A591 near Dale Bottom, GR 35/29.21. E. Sterne, 1984. 1st and 2nd records. **70**, Cumberland: Beacon Pike, GR 35/52.31. Moor. R. W. M. Corner, 1984, **LANC**. 2nd record. ***94**, Banffs.: Whiteash Wood, Fochabers, GR 38/35.57. Woodland rides. M. McC. Webster, 1983.

355/1. Arctous alpinus (L.) Nied. ***94**, Banffs.: Creag an Tarmachain, GR 38/15.31. Summit ridge. B.S.B.I. Meeting, 1983, **E**. **95**, Moray: Creag an Tarmachain, GR 38/15.31. Summit ridge. G. H. Forster & E. Norman, 1983, **E**. 2nd record.

359/3. Pyrola rotundifolia L. ***63**, S.W. Yorks.: Woolley Moor, GR 44/3.1. Boggy ground in wood. C. Hartley, 1977.

367/4×3. Primula elatior (L.) Hill×P. veris L. ***29**, Cambs.: Hayley Wood, GR 52/2.5. W. H. Palmer, 1980, **CGE**. 1st confirmed record.

†370/5. Lysimachia punctata L. ***77**, Lanarks.: Between Glasgow and Renfrew, GR 26/51.67. Shrubby waste ground. P. Macpherson & E. Teasdale, 1983. 1st record of naturalized population.

†378/2. Ligustrum ovalifolium Hassk. ***77**, Lanarks.: Cuningar Loop, GR 26/62.63. Waste ground. A. J. Silverside & A. McG. Stirling, 1981. Between Glasgow and Renfrew, GR 26/51.67. Shrubby waste ground. P. Macpherson & E. Teasdale, 1983, **herb. P. M.** 1st and 2nd records.

380/1. Cicendia filiformis (L.) Delarb. **4**, N. Devon: Meddon, GR 21/27.17. Damp track. W. H. Tucker, 1973, **EXR**. 2nd record.

383/1. Blackstonia perfoliata (L.) Huds. †***99**, Dunbarton: Ardmore, GR 26/3.7. Waste ground. C. M. Waltho, 1984, **E**, conf. A. McG. Stirling.

385/4. Gentianella anglica (Pugsl.) E. F. Warb. **4**, N. Devon: Braunton Burrows, GR 21/45.34. Dune slack. J. G. Keylock, 1973. 1st post-1930 record.

387/1. Nymphoides peltata (S. G. Gmel.) Kuntze †***45**, Pembs.: Scolton Home Farm, GR 12/99.22. Pond. T. Theobald & P. Tress, 1981. R. Alun, St David's, GR 12/75.25. Running water. S. B. Evans, 1984. 1st and 2nd records.

†392/2. Symphytum asperum Lepech. ***29**, Cambs.: Whittlesford, GR 52/46.47. Roadside. G. M. S. Easy, 1972, **CGE**.

392/6. Symphytum tuberosum L. **38**, Warks.: Shipston on Stour, GR 42/26.39. River-bank. D. Porter, 1983, **WAR**, det. G. A. Nelson. 2nd record.

†392/bul. Symphytum bulbosum C. Schimper ***4**, N. Devon: Webbery Cross, GR 21/49.26. Roadside. W. H. Tucker, 1982, det. A. C. Leslie. Gammaton Moor, GR 21/49.24. Roadside. W. H. Tucker, 1984. 1st and 2nd records.

†392/Hid. Symphytum 'Hidcote Blue' ***12**, N. Hants.: N. of Monk Sherborne, GR 41/60.57. Wood. P. H. Rollinson, 1983, **herb. A. Brewis**, det. A. C. Leslie.

†Amsinckia intermedia Fischer & C. A. Meyer ***38**, Warks.: Warwick, GR 42/29.65. Disturbed ground. M. M. Lowe, 1984, **WAR**, det. E. L. Swann.

400/3. Myosotis stolonifera (DC.) Gay ex Leresche & Levier ***83**, Midlothian: Between Harbour and Bell's Hills, GR 36/20.64. Wet flush. W. Bennett, 1984, **E**, det. D. R. McKean. 1st localized record.

406/1 ros. Calystegia sepium (L.) R. Br. subsp. roseata Brummitt ***77**, Lanarks.: Cathkin, GR 26/62.58. Roadside. E. L. S. Lindsay, P. Macpherson & A. McG. Stirling, 1983, **herb. P.M.**

406/1×†3. Calystegia sepium (L.) R. Br.×C. silvatica (Kit.) Griseb. ***38**, Warks.: Near Warwick, GR 42/27.62. Waste ground. J. C. Bowra, 1984, **herb. J.C.B.**, det. R. K. Brummitt.

411/1. Hyoscyamus niger L. †***77**, Lanarks.: Hyndland, Glasgow, GR 26/55.67. Waste ground. A. McG. Stirling, 1983.

413/1. Solanum dulcamara L. **103**, Mid Ebudes: Port Donain, Mull, GR 17/73.29. Base of cliff. R. Coomber, 1978. 2nd Mull record.

†415/1. Datura stramonium L. **99**, Dunbarton: Colquhoun St, Helensburgh, GR 26/29.82. Disturbed ground. A. Rutherford, 1984, **E**. Only extant record.

416/7. Verbascum nigrum L. †**73**, Kirkcudbrights.: East of Creebridge, GR 25/46.65. Rough ground. O. M. Stewart, 1984. 1st post-1930 record.

420/1. Linaria pelisseriana (L.) Mill. †***57**, Derbys.: Dunston Tip, Chesterfield, GR 43/36.74. M. C. Hewitt, 1984, **DBY**.

430/3. Veronica catenata Pennell **81**, Berwicks.: Hutton Castle, GR 36/89.54. Riverside rocks. M. E. Braithwaite, 1984, **herb. M.E.B.** 2nd record.

†430/21. Veronica persica Poir. **103**, Mid Ebudes: Tomain nan Eun, Coll, GR 17/17.55. Garden weed. J. W. Clark, 1984, **E**. 1st Coll record.

435/1/17×13. Euphrasia arctica Lange ex Rostrup×E. nemorosa (Pers.) Wallr. ***77**, Lanarks.: Meadowside, Glasgow, GR 26/55.66. Path. P. Macpherson, 1982, **herb. P.M.**, det. A. J. Silverside.

442/3. Utricularia intermedia Hayne **107**, E. Sutherland: 6 km SW. of Lairg, GR 29/52.02. Marsh. J. K. Butler, 1984, **E**. 2nd record.

445/3×†5. Mentha arvensis L.×M. spicata L. ***77**, Lanarks.: R. Calder near East Kilbride, GR 26/64.51. River bank. E. L. S. Lindsay & P. Macpherson, 1982, **herb. P. M.**, det. R. M. Harley. 1st localized record.

445/4×3. Mentha aquatica L.×M. arvensis L. ***79**, Selkirks.: Ettrick Water, Howden, GR 36/44.27. River bank. R. W. M. Corner, 1983, **herb. R.W.M.C.**, det. R. M. Harley. 1st localized record.

445/4×†5. Mentha aquatica L.×M. spicata L. **103**, Mid Ebudes: Salne, Mull, GR 17/57.43. Marsh. R. W. M. Corner, 1983, **herb. R.W.M.C.**, det. R. M. Harley. 2nd record and 1st Mull record.

446/1. Lycopus europaeus L. **68**, Cheviot: R. Tweed near Northam, GR 36/89.46. River bank. G. A. & M. Swan, 1984. 2nd extant record.

451/2. Calamintha sylvatica Bromf. subsp. ascendens (Jordan) P. W. Ball **44**, Carms.: Laugharne, GR 22/30.10. Degraded sea cliffs. J. Rees, 1984, **NMW**, det. R. G. Ellis. Only extant record.

†454/1. Melissa officinalis L. **38**, Warks.: Near Binton, GR 42/14.53. Hedgerow. J. C. Bowra, 1983, **WAR**. 2nd record.

†459/1. Stachys annua (L.) L. **35**, Mons.: Chepstow, GR 31/52.93. Garden weed. T. G. Evans, 1984. 2nd record.

†475/4. Campanula lactiflora Bieb. ***94**, Banffs.: Ballindalloch, GR 38/17.37. B.S.B.I. Meeting, 1983.

†475/por. Campanula portenschlagiana Schultes **44**, Carms.: Llanddowros, GR 22/25.14. Steep bank. G. Hutchinson, 1983, **NMW**, det. R. G. Ellis. 2nd record.

483/2. Asperula cynanchica L. **38**, Warks.: Near Whichford, GR 42/31.33. Basic grassland. M. J. Senior, 1973, **WAR**. 2nd record.

485/3×4. Galium mollugo L.×G. verum L. ***72**, Dumfriess.: R. Nith Picnic Area, GR 26/83.05. J. D. S. Martin, 1984, **DFSM**, det. D. J. McCosh. ***80**, Roxburghs.: SW. of Hassendeanburn, GR 36/52.17. Roadside verge. R. W. M. Corner, 1984, **herb. R.W.M.C.**

487/1. Sambucus ebulus L. †**52**, Anglesey: Near Cae Owen, Llanbadrig, GR 23/38.94. Roadside verge. N. Wales Nat's Trust Survey Team, 1984. 1st post-1930 record.

†489/mic. Symphoricarpos microphyllus H.B.K. ***95**, Moray: Earlsmill, Darnaway, GR 28/97.55. Wood. M. McC. Webster, 1981, **E**, det. A. Evans.

†491/2. Lonicera japonica Thunb. **45**, Pembs.: Portfield, Haverfordwest, GR 12/94.15. E. C. Howells, 1984, **NMW**, det. R. G. Ellis. 2nd record.

494/2. Valerianella carinata Lois. **38**, Warks.: Snitterfield, GR 42/23.60. Roadside verge. M. J. Senior, 1984, det. P. J. Copson. 2nd record.

†496/1. Centranthus ruber (L.) DC. ***72**, Dumfriess.: R. Pow, Powfoot, GR 35/14.65. H. Darke, 1975, det. J. D. S. Martin.

497/2. Dipsacus pilosus L. ***14**, E. Sussex: SE. of Brightling Church, GR 51/69.20. Wood. L. B. Burt, 1980.

†503/1. Galinsoga parviflora Cav. ***4**, N. Devon: Appledore, GR 21/46.30. M. Tulloh, 1978, conf. J. J. Hayward. **50**, Denbs.: Acton, GR 33/34.51. Garden weed. J. B. Formstone, 1984. 2nd record.

†503/2. Galinsoga ciliata (Raf.) Blake **69**, Westmorland: Woodlands, Crooklands, GR 34/52.83. Nursery weed. G. Halliday, 1984, **LANC**. 2nd record.

†506/ver. Senecio vernalis Waldst. & Kit. ***95**, Moray: Hopeman, GR 38/14.69. Sandy ground. Inverness Botany Group, 1983, **CGE**, conf. J. W. Kadereit.

506/†ver.×8. Senecio vernalis Waldst. & Kit.×S. vulgaris L. ***95**, Moray: Hopeman, GR 38/14.69. Sandy ground. M. McC. Webster, 1983, **CGE**, conf. J. W. Kadereit.

†507/2. Doronicum plantagineum L. var. excelsum N. E. Brown ***70**, Cumberland: E. of Inglewood Bank, GR 35/53.34. Shaded roadside verge. R. W. M. Corner, 1984, **LANC**, det. A. C. Leslie. 1st record of species.

†512/6. Dittrichia viscosa (L.) W. Greuter ***25**, E. Suffolk: Landguard Common, Felixstowe, GR 62/28.31. Roadside. G. W. Maybury, 1982, det. E. J. Clement.

514/3. Filago pyramidata L. **13**, W. Sussex: Halnaker, GR 41/92.08. Chalk-pit. H. W. Matcham, 1983, det. C. Jeffrey. 1st record since 1905.

†518/3 ser. Solidago gigantea Ait. subsp. serotina (O. E. Kuntze) McNeill. ***77**, Lanarks.: Shields, Glasgow, GR 26/51.67. E. Teasdale & P. Macpherson, 1983, **herb. P. M.**, det. E. J. Clement.

†526/1. Anthemis tinctoria L. **44**, Carms.: Near Pant-yr-athro, Llansteffan, GR 22/36.12. Disturbed ground. I. K. Morgan, 1984, **NMW**, det. R. G. Ellis & T. G. Evans. 2nd record.

526/3. anthemis arvensis L. **80**, Roxburghs.: A7 S. of Hawick, GR 36/48.13. Disturbed roadside bank. R. W. M. Corner, 1984, **herb. R.W.M.C.** 1st record since 1873.

532/1. Matricaria recutita L. **77**, Lanarks.: Hyndland, Glasgow, GR 26/55.67. Disused railway. A. McG. Stirling, 1982. 2nd record.

†533/3. Leucanthemum maximum (Ramond) DC. **35**, Mons.: A 471 near road to Llanfair Kilgeddin, GR 32/34.06. Roadside. T. G. Evans, 1984. 2nd record. ***44**, Carms.: Llangennech, GR 22/55.01. Roadside. R. D. Pryce, 1974. Machynys, GR 22/51.97. Tip. I. K. Morgan, 1984, **NMW**. 1st and 2nd records.

†534/squ. Cotula squalida Hook. fil. ***94**, Banffs.: Ballindalloch, GR 38/17.37. Lawn. B.S.B.I. Meeting, 1983.

†536/exa. Echinops exaltatus Schrader: ***94**, Banffs.: Tomintoul, GR 38/16.19. Roadside verges. M. McC. Webster, 1983.

539/3. Carduus nutans L. ***94**, Banffs.: Laggan, Tomnavoulin, GR 38/21.26. M. Burnhill, 1982.

540/1. Cirsium eriophorum (L.) Scop. **35**, Mons.: Near Castle Burness Quarry, GR 31/45.88. P. Jones & C. Titcombe, 1984. Only extant record.

†544/2. Centaurea montana L. ***49**, Caerns.: N. Pont Farchwell, GR 23/76.69. Roadside verge. R. Lewis, 1984, **NMW**. ***94**, Banffs.: Tomintoul, GR 38/16.19. Roadside verges. M. McC. Webster, 1983.

547/1. Lapsana communis L. **103**, Mid Ebudes: Tomain nan Eun, Coll, GR 17/17.55. Garden. J. W. Clark, 1984. 1st Coll record.

551/2. Picris hieracioides L. †***99**, Dunbarton: Duntocher, Glasgow, GR 26/49.72. Among grass. A. McG. Stirling, 1984, **E**.

†552/2. Tragopogon porrifolius L. **35**, Mons.: R. Wye opposite Woodcroft Cliffs, GR 31/53.96. River bank. D. Upton, 1984. 2nd extant record.

554/1. Lactuca serriola L. †***4**, N. Devon: Croyde, GR 21/45.38. Waste ground. M. Tulloh, 1969. Bideford, GR 21/45.25. Disturbed ground. W. H. Tucker, 1974. 1st and 2nd records.

†558/1/3. Hieracium speluncarum Arv.-Touv. ***59**, S. Lancs.: N. of Darwen, GR 34/69.22. Wall. P. Jepson, 1982, **LIV**, det. P. D. Sell.

558/1/18. Hieracium lingulatum Backh. ***94**, Banffs.: Coire Raibeirt, Cairn Gorm, GR 38/00.02. Rocks. R. Fitzgerald, 1983, **E**, det. P. D. Sell.

558/1/24. Hieracium pseudanglicum Pugsl.: ***94**, Banffs.: Coire Raibeirt, Cairn Gorm, GR 38/00.02. Mountain ledge. R. Fitzgerald, 1983, **E**, det. D. J. Tennant.

558/1/45. Hieracium lasiophyllum Koch ***78**, Peebless.: Codleteth Burn, Talla, GR 36/14.21. Rock ledges. D. J. McCosh, 1978, **herb. D.J. McC.**

558/1/99. Hieracium grandidens Dahlst. ***94**, Banffs.: Ballindalloch, GR 38/17.37. M. McC. Webster, 1983, **E**, det. P. D. Sell.

558/1/120. Hieracium subhirtum (F. J. Hanb.) Pugsl. ***94**, Banffs.: Loin Bridge, Glen Avon, GR 38/12.06. Riverside rock. R. Fitzgerald, 1983, **E**, det. P. D. Sell.

558/1/206. Hieracium latobrigorum (Zahn) Roffey ***78**, Peebless.: Neidpath Castle, Peebles, GR 36/23.40. Riverside rocks. D. J. McCosh, 1981, **herb. D.J.McC.**

558/1/pse. Hieracium pseudanglicoides J. E. Raven, P. D. Sell & C. West ***94**, Banffs.: Allt Loin Beag, Glen Avon, GR 38/13.06. Burnside rocks. M. McC. Webster, 1983, **E**, det. P. D. Sell.

558/2/1 eur. Hieracium pilosella L. subsp. euronotum Naegeli & Peter ***94**, Banffs.: Kilnmaichlie, GR 38/18.33. Short grass. B.S.B.I. Meeting, 1983, det. O. M. Stewart.

558/2/1 tri. Hieracium pilosella L. subsp. trichosoma Peter **103**, Mid Ebudes: Cliad, Coll, GR 17/20.59. Rock outcrop. J. W. Clark, 1984, **E**, det. A. McG. Stirling.

†559/2. Crepis vesicaria L. subsp. haenseleri (Boiss. ex DC.) P. D. Sell ***77**, Lanarks.: Shieldhall, Glasgow, GR 26/53.65. Long grass. P. Macpherson, 1984, **herb. P.M.**

†570/3. Elodea nuttallii (Planch.) St. John ***4**, N. Devon: Chenson Farm Pond, Chawleigh, GR 21/70.09. P. M. Williams, 1977. Grand Western Canal SW. of Halberton, GR 21/99.12. L. J. Margetts, 1984, **herb. L.J.M.** 1st and 2nd records. ***26**, W. Suffolk: New Cut, Mildenhall, GR 52/72.75. O. M. Stewart & M. McC. Webster, 1983, **herb. E.M. Hyde**, det. D. A. Simpson. ***38**, Warks.: R. Avon near Warwick, GR 42/27.62. J. C. Bowra, 1984, **WAR**. R. Leam, Leamington Spa, GR 42/31.65. J. C. Bowra, 1984. 1st and 2nd records, both det. P. Stafford. ***44**, Carms.: Upper Trebeddod Reservoir, Llanelli, GR 22/50.02. I. K. Morgan, 1982. Afon Teifi, Henllan, GR 22/36.40. B. Gale & J. Killick, 1984. Both **NMW**, det. R. G. Ellis. 1st and 2nd records. ***67**, S. Northumb.: Holywell Pond, GR 45/32.75. G. A. Swan, 1984, **herb. G.A.S.**, conf. D. A. Simpson.

†571/1. Lagarosiphon major (Ridl.) Moss ***25**, E. Suffolk: Ipswich, GR 62/15.46. Ponds. M. A. Hyde, 1981, **herb. M.A.H.**, conf. E. J. Clement.

576/1. Zostera marina L. ***35**, Mons.: Severn Estuary off Caldicot Rifle Range, GR 31/47.85. Water channels in gravel beds. T. G. Evans, C. Titcombe & D. Upton, 1984, **herb. T.G.E.**, det. T. G. Tutin.

576/3. Zostera noltii Hornem. *35, Mons.: Severn Estuary off Caldicot Rifle Range, GR 31/47.85. Upper gravel beds. T. G. Evans, C. Titcombe & D. Upton, 1984, **herb. T.G.E.**, det. T. G. Tutin.

577/6. Potamogeton gramineus L. **72**, Dumfriess.: Mill Loch, Lochmaben, GR 35/07.83. M. E. R. Martin, 1984, det. N. T. H. Holmes. Only extant record.

577/7. Potamogeton alpinus Balb. *__51__, Flints.: Near Criccin Farm, Rhuddlan, GR 33/04.77. Pond. J. A. Green, 1977, **herb. G. Wynne**, det. N. T. H. Holmes. *__107__, E. Sutherland: Glass Hill burn, Brora, GR 29/81.16. E. Charter, 1984, **E**.

577/8. Potamogeton praelongus Wulf. *__72__, Dumfriess.: Upper Loch, Lochmaben, GR 35/07.83. M. E. R. Martin, 1984, det. N. T. H. Holmes.

557/14. Potamogeton obtusifolius Mert. & Koch *__44__, Carms.: Southern Lake, Talley, GR 22/63.33. I. K. Morgan, 1983, **NMW**, det. N. T. H. Holmes. *__107__, E. Sutherland: Loch Dola Lairg, GR 29/60.07. E. Charter, 1984, **E**.

577/15. Potamogeton berchtoldii Fieb. **107**, E. Sutherland: Loch Arichlinie, GR 29/85.35. E. Charter, 1984. 2nd record.

580/1. Zannichellia palustris L. *__95__, Moray: Spynie Loch, GR 38/23.66. B. Gerrie, 1978, **ABD**.

589/3. Polygonatum multiflorum (L.) All. †**49**, Caerns.: N. side of Afon Dulyn, Talybont, GR 23/76.68. R. Lewis, 1984. 2nd record.

†593/1. Lilium martagon L. **41**, Glam.: Bute Park, Cardiff, GR 31/1.7. V. G. Ellis, 1983, **NMW**. 2nd record.

†600/2. Hyacinthoides hispanica (Miller) Rothm. **49**, Caerns.: N. side of Afon Dulyn, Talybont, GR 23/76.68. R. Lewis, 1984. 2nd record.

605/amb. Juncus ambiguus Guss. *__101__, Kintyre: Keills, GR 16/69.80. Dried pools on shore. Barrahormid, GR 16/71.83. Dried pools on shore. Both A. G. Kenneth, 1984, **LTR**, det. C. A. Stace. 1st and 2nd records.

605/fol. Juncus foliosus Desf. *__101__, Kintyre: N. of Keillmore, GR 16/69.80. Ditch. A. G. Kenneth, 1984, **LTR**, det. C. A. Stace.

†606/4. Luzula luzuloides (Lam.) Dandy & Wilmott *__46__, Cards.: Maestir churchyard, GR 22/55.49. Grassland. A. O. Chater, 1984.

607/3. Allium scorodoprasum L. †*__77__, Lanarks.: Biggar, GR 36/04.37. M. Allan, 1980, det. E. J. Clement. **81**, Berwicks.: English border, Paxton, GR 36/94.52. Lane bank. M. E. Braithwaite, 1984, **herb. M.E.B.** 2nd record.

†607/7. Allium carinatum L. *__70__, Cumberland: Inglewood Bank, GR 35/53.34. R. W. M. Corner, 1984, **LANC**.

612/†elw.×1. Galanthus elwesii Hook. f.×G. nivalis L. *__17__, Surrey: Henley Park, Normandy, GR 41/93.52. A. C. & J. F. Leslie, K. W. Page & E. V. Pilcher, 1984, **herb. A.C.L.**, conf. C. D. Brickell.

†616/sib. Iris sibirica L. *__96__, Easterness: Lochloy, Nairn, GR 28/92.57. Edge of copse. M. McC. Webster, 1982.

636/1b. Gymnadenia conopsea (L.) R. Br. subsp. densiflora (Wahlenb.) G. Camus, Bergon & A. Camus *__44__, Carms.: Laugharne Burrows, GR 22/27.07. Dune slack. J. Rees, 1984, **NMW**, det. S. B. Evans & R. D. Pryce.

643/3b. Dactylorhiza incarnata (L.) Soó subsp. pulchella (Druce) Soó *__103__, Mid Ebudes: Port na Tairbeirt, Mull, GR 17/74.29. Flush. A. McG. Stirling, 1984, **E**.

†648/1. Lysichiton americanus Hultén & St. John **49**, Caerns.: Afon Rae between Talybont and Tyn-y-groes, GR 23/76.69. Base of river bank. R. Lewis, 1984. 2nd record.

649/1. Arum maculatum L. **103**, Mid Ebudes: Tobermory, Mull, GR 17/50.55. Shady bank. A. Wright, 1984. 2nd record.

†649/2 ita. Arum italicum Mill. subsp. italicum ***46**, Cards.: Henllan churchyard, GR 22/35.40. Hedgebank. A. O. Chater, 1984.

649/2 neg. Arum italicum Mill. subsp. neglectum (Townsend) Prime †***29**, Cambs.: Granhams Road, Cambridge, GR 52/46.53. Roadside verge. N. G. Hodgetts, 1984, **CGE**.

650/2. Lemna trisulca L. ***45**, Pembs.: Mere Pool, Broad Haven, Bosherston, GR 11/97.94. Reedswamp. S. B. Evans, 1984.

†650/minus. Lemna minuscula Herter ***12**, N. Hants.: Longstock Water Gardens, GR 41/37.37. E. G. Philp, 1983. **25**, E. Suffolk: Ipswich, GR 62/17.43. Canal. F. W. Simpson, 1983, conf. A. C. Leslie. 2nd record.

652/3. Sparganium angustifolium Michx. **94**, Banffs.: Cairn Gorm, GR 38/00.00. Pool. D. Batty, 1983. 1st post-1930 record.

653/2×1. Typha angustifolia L.×T. latifolia L. ***17**, Surrey: Ashtead Park, GR 51/19.58. Pond. A. C. & J. F. Leslie, 1983, **herb. A.C.L.** ***29**, Cambs.: R. Great Ouse, Littleport, GR 52/57.87. Base of embankment. A. C. Leslie, 1984, **CGE**.

656/6. Eleocharis uniglumis (Link) Schult. ***12**, N. Hants.: Chilbolton Common, GR 41/38.40. Pasture. R. B. Gibbons, 1979. North Warnborough Common, GR 41/72.52. F. Rose, 1983. 1st and 2nd records.

658/1. Cyperus longus L. †***38**, Warks.: Red Hill near Billesley, GR 42/13.56. Roadside verge. J. A. Hardman, 1973.

663/15. Carex pseudocyperus L. **4**, N. Devon: R. Torridge S. of Torrington, GR 21/49.17. River-bank. M. Tulloh, 1966. 2nd record.

663/17. Carex vesicaria L. **45**, Pembs.: Gwaun Valley 2 km E. of Pontfaen, GR 22/04.34. Fen. C. Chadwell, 1984. 2nd record.

663/22. Carex pendula Huds. †**94**, Banffs.: Ballindalloch, GR 38/17.37. B.S.B.I. Meeting, 1983. 1st post-1930 record.

663/30. Carex rariflora (Wahlenb.) Sm. **94**, Banffs.: Lochan Buidhe, Ben Macdui, GR 28/98.01. Damp flush at 1125 m. M. B. Usher, 1983. 1st post-1930 record.

663/47. Carex acuta L. ***4**, N. Devon: Hole Stock Bridge, Northlew, GR 21/48.00. Waterlogged meadow. W. H. Tucker, 1971, **EXR**, det. R. Ross. **81**, Berwicks.: R. Tweed, Paxton, GR 36/94.52. Edge of river. M. E. Braithwaite, 1984, **herb. M.E.B.** 2nd extant record.

663/54×71. Carex paniculata L.×C. remota L. ***101**, Kintyre: S. of Craiglin, GR 16/7.8. Ditch. A. G. Kenneth, 1984, **BM**, det. A. C. Jermy.

663/56. Carex diandra Schrank **45**, Pembs.: Maendewi Pool, Dowrog, GR 12/76.26. Fen. R. E. Smith, 1983, **BM**, det. A. O. Chater & A. C. Jermy. 2nd record.

663/57. Carex otrubae Podp. ***43**, Rads.: Between Pistyll and Glasbury, GR 32/16.39. Damp roadside verge. R. G. Woods, 1984, **NMW**.

663/64. Carex maritima Gunn. **85**, Fife: St Andrews Links, GR 37/50.17. Dune slack. S. J. Leach, 1984. Only extant record.

663/72. Carex curta Gooden. **4**, N. Devon: 3·5 km SW. of Woolfardisworthy, GR 21/30.19. Wet moor. W. H. Tucker, 1973, **EXR**, det. A. C. Jermy. 2nd record.

663/73. Carex lachenalii Schkuhr **92**, S. Aberdeen: Cairn Toul, GR 27/95.97. D. J. Tennant, 1975, **BM**, det. A. O. Chater & R. W. David. Only extant record.

669/1×2. Glyceria fluitans (L.) R. Br.×G. plicata Fr. ***99**, Dunbarton: R. Clyde S. of Bowling, GR 26/45.73. R. Mackechnie, 1932, **E**, det. J. E. Lousley.

669/2. GLYCERIA PLICATA Fr. *77, Lanarks.: R. Kelvin, Bunhouse, Glasgow, GR 26/56.66. J. H. Dickson, 1984, **herb. J.H.D.** *99, Dunbarton: Garscadden Burn, Glasgow, GR 26/5.7. Marsh. P. Macpherson & A. McG. Stirling, 1984, **E**.

670/9. FESTUCA TENUIFOLIA Sibth. **103**, Mid Ebudes: Beinn Feall, Coll, GR 17/14.54. Dry bank. J. W. Clark, 1984, **E**, det. A. McG. Stirling. 1st Coll record.

673/3 bor. PUCCINELLIA DISTANS (L.) Parl. subsp. BOREALIS (Holmberg) W. E. Hughes **83**, Midlothian: Granton, GR 36/26.76. O. M. Stewart, 1977. 2nd record.

675/1. VULPIA UNILATERALIS (L.) Stace *25, E. Suffolk: Barham, GR 62/1.5. Eroded scree in gravel pits. J. W. Digby, 1983, **IPS**, conf. C. A. Stace.

†676/14. POA PALUSTRIS L. *94, Banffs.: Bridge of Brown, GR 38/12.20. Damp ledge near burn. B.S.B.I. Meeting, 1983, **E**, det. M. McC. Webster.

677/1. CATABROSA AQUATICA (L.) Beauv. 44, Carms.: Llandeilo-abercowin, Llanybri, GR 22/31.12. Marsh. H. Adams, 1984, **NMW**, 2nd record.

683/3. BROMUS BENEKENII (Lange) Trimen *50, Denbs.: Ceiriog valley near Pandy, GR 33/1.3. Wood. P. M. Benoit & E. D. Pugh, 1984, **NMW**.

†683/4. BROMUS INERMIS Leyss. **99**, Dunbarton: Garscadden, Glasgow, GR 26/52.70. Waste ground. A. McG. Stirling, 1984, **E**, det. P. J. O. Trist. 2nd record.

683/15. BROMUS COMMUTATUS Schrad. **72**, Dumfriess.: Jericho Loch, Locharbridge, GR 25/99.80. Gravel bank. M. E. R. Martin, 1984, **DFSM**, det. P. J. O. Trist. 1st post-1930 record.

†683/19. BROMUS CARINATUS Hook. & Arn. *51, Flints.: Thornleigh Park, GR 33/36.66. Farmyard. G. Wynne, 1982, **herb. G. W.**, det. P. J. O. Trist.

†692/1. AVENA FATUA L. **99**, Dunbarton: A82, Old Kilpatrick, GR 26/46.73. Roadside verge. A. McG. Stirling, 1983. 2nd record.

†697/3. AIRA CARYOPHYLLEA L. subsp. MULTICULMIS (Dumort.) Bonnier & Layens **94**, Banffs.: R. Spey, Ballindalloch, GR 38/17.37. River shingle. M. McC. Webster, 1983, **E**. 2nd record.

†PANICUM MILIACEUM L. *99, Dunbarton: Ardoch, Cardross, GR 26/36.76. Roadside verge. A. McG. Stirling, 1984, **E**.

†719/2. DIGITARIA SANGUINALIS (L.) Scop. *51, Flints.: Coed Duon, Tremeirchion, GR 33/07.71. J. A. Green, 1983, **herb. G. Wynne**, det. P. J. O. Trist.

†720/1. SETARIA VIRIDIS (L.) Beauv. **44**, Carms.: Cwmgwili, GR 22/57.09. Roadside. G. Hutchinson, 1984, **NMW**, det. R. G. Ellis. 2nd record.

Book Reviews

A list of the photographs in the R. J. Welch collection in the Ulster Museum. Volume 2. Botany, Geology and Zoology. P. Hackney, K. W. James & H. C. G. Ross. Pp. 36. Ulster Museum, Belfast. 1983. Price £1·50 including postage (ISBN 0–900761–14–8).

Robert John Welch was born in 1859 at Strabane, Co. Tyrone. He was not only the most noted photographer of his day in Ireland but was also an amateur naturalist of considerable repute. His photographs, in the form of glass negatives, were left to the Belfast Naturalists' Field Club upon his death in 1936 and thence passed to the Ulster Museum. Many of these photographs will be familiar to readers of *The botanist in Ireland* (1934) by R. Ll. Praeger, and other publications on Irish natural history. More recently a selection of them has been published in a biographical volume, *Ireland's Eye: the photographs of R. J. Welch* (1977) by E. Estyn Williams and B. S. Turner. The first part of the present catalogue (*Volume 1. Topography*) was issued in 1979.

In *Volume 2* some 460 entries (rather over a third of the total) relate to botanical, including horticultural, subjects. Each entry has a reference number and published photographs are cross-referenced to their place of publication. A welcome bonus is a bibliography of the nearly 180 articles that Welch contributed to journals of Irish natural history, especially in his principal field of conchology: the papers listed include observations on antiquities, fish, reptiles, sand-dunes, snails, woodlice and other heterogeneous topics!

This slim volume, simply but attractively laid out in A4 format, is a useful and thorough work of reference and is most reasonably priced. It is to be hoped that the reader will be tempted to purchase some of the prints (available from the Museum) in order to possess such evocative images of Ireland's sad, beautiful countryside and its fascinating natural history.

J. R. Akeroyd

The English plant names in The Grete Herball (1526). Mats Rydén. Pp. 110. Almqvist & Wiksell International, Stockholm, Sweden. 1984. Price SwKr 92 (ISBN 91–22–00710–5; ISSN 0346–6272).

This scholarly book, which is No. LXI in the series *Stockholm Studies in English*, is an analysis of the English plant names in *The Grete Herball* (1526). Following a similar project on Swedish plant name usage and other recent Scandinavian work on English plant names, this book gives information on very early derivations of some English plant names familiar to us today. Some of these were first recorded in *The Grete Herball*, the second earliest English printed herbal, which gives English names for more than 500 plants, fruits and spices. The author claims that this most important document in the history of English plant name usage has not been submitted previously to a systematic analysis; and he reminds us that the early herbals, which were possibly the most widely read books of their day, are storehouses of old popular plant names. *The Grete Herball*, in content and style a mediaeval document, is a translation from the French *Le grant herbier*, which was first published in 1486–88 as *Arbolayre*; this in turn was derived from the 12th century Latin manuscript *Circa instans*.

For his analysis, the author has consulted the English *Grete Herball* editions 1526–1561 and the earlier French herbal. The plants included are those which were known at the time for their medicinal or culinary use, with some which had "stirred the imagination" from England and "beyond the sea". Botanical information is limited, but examples of plant and habitat descriptions often have a descriptive phrase on growth habit or a plant character which we would recognize today and which links with life in mediaeval times. As a plant-name researcher the author has analysed the continuity and discontinuity of the English names and their synonymy, from the early herbals to a final comparison with those used in *Flora of the British Isles* by Clapham, Tutin & Warburg, 2nd ed. (1962). Of the 500 English names in *The Grete Herball*, the author has listed

175 that are also in 'C.T.W.'. Plants that have several English names can cause confusion today – in the 1526 work 40% had more than one English name and six plants have three or more.

The author establishes the origin of most of these names by reference to their earlier and later occurences in English records. Many of the names are direct translations from the French, but some are independant additions or parallel names from earlier texts, and 100 are of Old English descent; this suggests that the anonymous translator had a considerable knowledge of English plant names. More than half of those in *The Grete Herball* are first attested in Middle English sources, and many antedate the earliest entries in the *Oxford English Dictionary*. Some 90 of the names are Mats Rydén's own first-record discoveries. The most difficult problems are the identification and plant-name equivalence, and some names still remain dubious. These problems are outlined in the text, as are the methods and history of the study, with much detailed information on *The Grete Herball*. Additionally there is a bibliography and three tables, of which one is the overall list of the English plant names in this herbal under four headings: name in *Grete Herball*, modern form, Latin headings in *Grete Herball*, and modern scientific name.

Included in the acknowledgments is D. E. Allen, B.S.B.I. historian, and the author also refers to "many inspiring discussions with the late Miss Blanche Henrey". Those with a love of words and a love of plants must surely find this a fascinating book. It is announced as the first part of a project on the plant names in early modern English herbals and floras, and we look forward with anticipation to subsequent studies in the series.

M. Briggs.

Our green and living world – The wisdom to save it. E. S. Ayensu, V. H. Heywood, G. L. Lucas and R. A. DePhillips. Cambridge University Press, Cambridge. 1984. Pp. 256 with numerous colour photographs. Price £12.95. (ISBN 0–521–26842–7).

It is a truism that both conservationists and the general public are much better informed about, and involved with, the conservation of animals than plants. No doubt this is partly due to the photogenic qualities of the animal kingdom that we see reflected weekly on our television screens. It is easy to identify with a cuddly mammal or to envy the mastery of the air displayed by some of the birds. With the noble exceptions of David Bellamy and a very few others, our TV naturalists have failed to give plants the attention and credit that is their due. As the ultimate source of all the Earth's food resources, plants deserve a better press; and, unless they get it, we are likely to suffer along with the rest of the Animal Kingdom. A notable consortium of British and American botanists has attempted in this book to strike a firm blow to redress the balance, coupled with the related aim of lifting the eyes of those living in the North Temperate regions beyond conservation on their own doorsteps, to the even more demanding and critical problems in the arid areas and rain forests adjacent to the equator. At first glance, it may appear to be yet another Natural History book for the coffee tables of the western world; but, while it is indeed sumptuously illustrated in colour with photos that are often of strikingly high quality, it also has a text that is serious, authoritative and challenging.

The book is divided into five parts. In the first, man's relationship with plants are traced from the dawn of history till the present time. Then follows descriptions of the major plant community types that cover the earth. The level of treatment is somewhat uneven, and the chapter covering marine habitats is frankly inadequate and will do little to dispel the general ignorance of seaweeds among otherwise well-informed terrestrial naturalists. On the other hand, the chapters on Mediterranean regions and tropical forests are informative, interesting and have a clear conservation message. Next comes a group of chapters on the current use of plants by man, ranging from the basic subsistence needs of primitive communities to the sophisticated involvement of compounds produced by plants in the most advanced forms of western medicine. It may come as a surprise to learn that for some people living on a borderline economy the firewood needed to render food palatable and digestible is an even scarcer commodity that the food itself. Part IV reviews what needs to be done as a matter of international urgency, if the remainder of the earth's legacy of botanical bounty is to be preserved for future generations. This is a question that no thinking person can neglect at any level, from genetic resources for crop plants to the aesthetic values that should illuminate the lives of our children's children – always supposing that they have the time and energy left over from scratching a living from a ravaged planet to appreciate them. In the final section, a list of selected readings, a statement of the World Conservation Strategy and an index are provided. It has been a particularly poignant experience to review this book, at a time when some of its contents have been starkly illuminated by the famine in Ethiopia, and when the assassination of Mrs Gandhi, who contributed a thoughtful epilogue to the book, has monopolized the attention of the world's media. Some aspects of her period as India's Prime Minister may be open to question; but very few of the major international politicians appear to have any grasp of the world conservation questions, and we cannot afford to lose any of them.

This is a good book. It does show some signs of having been put together rather hurriedly and there are a few errors, as in the confusing statement about redwoods and sequoias on page 81; but, in view of the urgency of our predicament, it is perhaps churlish to complain on this score. In the last analysis, it is governments, not individual conservationists and societies, that can have an effect on the scale that is needed. All members of the B.S.B.I. should be contributing towards a climate of opinion that will influence our Governments to exert maximum efforts in the world arena towards the conservation of man's environment. To do this to the best possible effect, you will need to be well informed; and I know of no easier and more effective way of improving your understanding of plant conservation on the global scale than by reading this book. You should get it, read it and put its message into good effect in your life and the lives of those around you. At £12.95 it is reasonably priced and should be accessible to all our membership.

J. F. M. CANNON

Flora of inner Dublin. P. Wyse Jackson and M. Sheehy Skeffington. Pp. x+174, with 13 pages of drawings. Royal Dublin Society, Thomas Prior House, Ballsbridge, Dublin. Prices IR£10.00 (hardback; ISBN 0–86027–01507); IR£5.00 (paperback; ISBN 0–86027–016–5).

This Flora is largely based on field work by the Dublin Naturalists' Field Club in 1979–1981. The main part of it is an extensively annotated list recording the distribution and status during these years of 357 species in 14 zones which are defined on the clear maps on the end papers. The history of the flora is brilliantly covered in a long chapter by D. Doogue which contains much about the development of Irish botany and the city of Dublin as well as unexpected details about many of the species. It is a pity that this chapter is not indexed, as much in it is complementary to the information in the list and the two do not always tally (*Spergularia rupicola*, for example, is unaccountably missing from the list though mentioned as still present by Doogue). A chapter by the main authors describes a number of sites in detail and should enable any botanist visiting Dublin to occupy his time profitably. In other chapters M. S. Skeffington discusses the cultivated and naturalized plants, and J. R. Akeroyd gives a valuable general discussion on weeds and their strategies as well as describing particular weed habitats in the city. The bryophytes are briefly surveyed, with 31 species listed, and the lichen literature is summarized. The text is enlivened by evocative drawings of plants in the most extreme urban habitats. The bibliography of 81 items is mostly confined to the Dublin literature.

There have been comparatively few published surveys of entire urban floras, and this book should act as a model for further work. The authors emphasise the constant changes in the city environment, and as their list is very much a 'snapshot' of the flora in the 3-year period of the survey, it will be of great interest to repeat the survey at intervals. (It would also be interesting to compare the Dublin flora with that of cities elsewhere.) As striking as the changes, however, is the persistence of many species, for example those of woodlands or the sea coast, in highly artificial urban habitats for decades or even centuries after their natural habitats have vanished from the neighbourhood.

This delightful Flora, which may be said to do Dublin for the botanist as *Ulysses* does it for the common reader, is unreservedly recommended.

A. O. CHATER

Directory of important world honey sources. E. Crane, P. Walker and R. Day. International Bee Research Association. 1984. Pp. 384. Obtainable from IBRA, Hill House, Gerards Cross, Bucks., SL9 0NR, U.K. Price £27.50. (ISBN 0–86098–141–X).

This directory identifies 467 plants that are reported as major honey sources by honey-producing areas of the world; 452 produce nectar and 15 support honeydew-secreting insects. Of the plants surveyed for inclusion, nearly one third belong to the families Leguminosae, Myrtaceae and Compositae. For each source plant, details are given of its distribution, habitat, economic uses, flowering period, nectar or honeydew flow, its honey and pollen production and, where known, the properties of the resulting honey.

Warnings are given where plants have become a nuisance when introduced to new localities or where they cause beekeeping problems. For example, *Echium lycopsis* L., "Patterson's Curse", a major honey source in arid Australia, is a rampant weed in wetter areas and a problem to honey producers because of the high sucrose content of its honey.

Entries in this word-processor-compiled book have been coded to allow searches to be made for plants with particular characteristics. The results of seven such searches are reproduced and include lists of honey sources tolerant of drought and salt, 'problem' plants, and sources of honey with four properties important to commercial producers.

The directory is not yet complete but, even so, it will provide guidance in selecting plants for introduction with suitable cultural or honey characteristics. It could also prevent the eradication in land-improvement schemes of native 'scrub' plants of importance to honey producers and probably to many foraging insects not of economic importance.

J. Dolling

The Northwest European Pollen Flora IV. W. Punt & G. C. S. Clarke (editors). Pp. 370, with 169 b. & w. plates. Elsevier, Amsterdam. 1984. Price Dfl. 190·00, US$73·00. (ISBN 0–444–42405–9).

Volume 4 of the above work includes accounts of the pollen morphology of ten complete families: Araliaceae, Berberidaceae, Cannabaceae, Moraceae, Urticaceae, Fagaceae, Hippocastanaceae, Menyanthaceae, Plumbaginaceae and Umbelliferae, as well as Compositae – tribe Lactuceae (Cichorieae). The format of previous volumes is closely followed, and the work is again a hard-covered reprint from the *Review of Palaeobotany and Palynology*.

The most outstanding feature of this volume, which occupies almost two-thirds of the pages, is the account of the Umbelliferae. This is the first really large family to be treated in its entirety for this Pollen Flora. The account incorporates over 100 taxa, in which some 50 pollen types are described and keyed and illustrated by no less than 95 plates of almost 750 micrographs. Dr Punt must be congratulated on grappling with this truly mammoth task and producing a very clear and excellent account of this important family. The definitions of terms and the review of Mme Cerceau-Larrival's classic account of the pollen of the family are especially useful features. I hesitate to make any critical comment, but many of the SEM micrographs, especially the detail of the ornamentation, are not of as high a standard as we have come to expect today.

Dr Blackmore's account of Lactuceae is the second largest contribution, covering some 60 taxa in 7 pollen types. This is a highly competent and nicely presented treatment with valuable and carefully drawn diagrams and explanations of the terminology. The work is marred only by some singularly gloomy micrographs, Plate II (page 64) being notable. It might be appropriate to suggest here that attention must be given in future volumes to the printed quality of the half tones.

The Fagaceae is a family for which an account will no doubt be welcomed by pollen analysts. However, personally, I find the characters in the pollen key used to distinguish *Quercus* species a little subtle; and I take the authors' word that they can reliably separate species in the *Quercus robur* and *Q. rubra* groups (or in fact the groups themselves) and wonder if pollen analysts will attempt to distinguish all species.

The Cannabaceae, Moraceae and Urticaceae are combined because of the similarity of the pollen, and this is probably a helpful departure from the usual format. Here I would have liked to see SEM fractures or sections across the pori of *Humulus* and *Cannabis* to elucidate these structures even more clearly. Such techniques are now relatively easily achieved with minimum equipment, and the fractures showing exine stratification, as used in *Fagus*, *Armeria*, *Ceratostigma* and *Oenanthe*, might be a regular feature that the editors could consider for future volumes. How interesting an SEM fracture showing the exine stratification of *Morus* would have been, as the light micrographs and descriptions still leave the reviewer perplexed! Where interference or phase-contrast light microscopical techniques are used, it would be helpful to state this in the plate legends, the micrographs on pages 12(2) and 127(1–2) being cases in point.

Fellow taxonomists would support me, I feel sure, in preferring to see pollen slides backed by herbarium voucher specimens, even of very common species, in a work of this high standard rather than such citations as "Fresh material Anno 1979".

Errors are few, but regrettably the reviewer's own collection *"Ferguson & Ferguson 3216"* (p. 125), cited in the plate legend, fails to appear in the "specimens examined". The specimen in question was collected in Britain: Sussex, 1971, **BM!**

The editors are to be congratulated on maintaining the high standards set in earlier volumes and in fact on constantly striving to improve many details. I feel certain that this fourth volume has now set the *Northwest European Pollen Flora* on course to becoming a reference work of major significance for both pollen analysis and plant taxonomy alike. As it is substantially larger than earlier volumes, the cost is therefore relatively less. However, it is still regrettably beyond the pocket of many workers.

I. K. Ferguson

Phytochemical methods, 2nd edition. J. B. Harborne. Pp. xii+288, with numerous text figures. Chapman & Hall, London. 1984. Price £17·50 (ISBN 0–412–25550–2).

The first edition of this book appeared in 1973 and was reviewed in *Watsonia*, **10**: 309 (1975). Since then, there have been a number of major developments in phytochemical techniques, including the use of nuclear magnetic resonance spectroscopy and high-performance liquid chromatography. The second edition of *Phytochemical methods* deals with these and other, more conventional, methods of chemical analysis in its discussion of six major classes of plant chemical, viz. phenolic compounds, terpenoids, organic acids and lipids and relatives, nitrogen compounds, sugars and derivatives, and finally, macromolecules. It can be seen that there is a heavy 'organic' emphasis, so much so that, unfortunately, the whole topic of the chemical composition of crystals in plants is omitted. I was also disappointed to find in the chapter on phenolic compounds a heavy emphasis placed on the techniques of paper chromatography for the identification of flavonoids. In my experience, at least for taxonomic purposes, these techniques are far inferior to those that employ thin layers of polyamide; the latter methods are both quicker and much more sensitive, and yet they barely get a mention.

The book does however, in general, give a good introduction, at the undergraduate level, to the methods of plant chemical identification and should be of value to the student embarking on a phytochemical study.

R. J. Gornall

The IUCN/WWF Plants Conservation Programme 1984–85. Pp. 28, with 22 b. & w. photographs, 2 tables and 4 maps. World Conservation Strategy, Occasional Paper No. 5. Price not stated. Available from World Wildlife Fund – U.K., Panda House, 11–13 Ockford Road, Godalming, Surrey GU7 1QU.

For many years, the public image of the World Wildlife Fund (WWF) has been focussed around the organization's conservation efforts with large mammals. Giant pandas, whales and tigers have had great public appeal and, perhaps understandably, many high-profile conservation efforts have been aimed at prominent examples of the animal kingdom such as these.

The importance of vegetation and its constituent parts in the conservation equation has long been recognized, even if it has been publicized less than it might have been in the media. However, between September 1982 and March 1984, the International Union for the Conservation of Nature and Natural Resources (IUCN) and WWF ran a Tropical Forest Campaign, the funds raised being used for field conservation projects in 17 countries. The success of the campaign has prompted the launch of a Plants Conservation Programme during 1984 and 1985, for which IUCN/WWF have produced this booklet.

Peter Raven contributes a Foreword aimed at encouraging botanists to play a more active role in conservation. The rest of the booklet is written by Hugh Synge and is arranged under seven sections. Under 'Spreading the Message', the aims of the campaign are outlined, not least of which are to raise public awareness of the importance of plants and IUCN/WWF's role in confronting a wider range of environmental issues. The second section explains the ways in which it is hoped to persuade other organizations to conserve plants, and the third concentrates on the vital issue of the conservation of plant genetic resources. Wild plants of economic importance are covered in the fourth section, and the role of botanic gardens in conservation is considered in the fifth. The sixth looks at the promotion of plant conservation in selected countries, and the last provides a useful summary of arguments in favour of plant conservation drawn from crop and medicinal plant examples, from plants with industrial and fuel uses and from threatened plant species.

Plants have been the poor relations of conservation for too long, at least in the public eye, and this important campaign is trying to take a first step to remedy the situation. I would strongly urge all B.S.B.I. members to read this booklet and support IUCN/WWF in whatever way possible.

C. E. Jarvis

Nature conservation in Britain. Anon. Pp. 112. Nature Conservancy Council, Shrewsbury. 1984. Price not stated (ISBN 0–86139–285–X). *Summary of objectives and strategy*. Pp. 15 (separately bound). Price not stated (ISBN 0–86139–284–1).

Government reports are frequently written in a defensive style that reveals little of the anonymous contributors or the Department that commissioned them. Caveats, exceptions, alternatives and numerous qualifying clauses shroud the factual data. This is not the case with the N.C.C.'s *Nature conservation in Great Britain*, which is concise and factual, yet very readable indeed. Its clear functional lay-out and typography help it to achieve its end in presenting the U.K.'s response to the World Conservation Strategy. It is presented in three parts: I. Aims, methods and achievements of Nature Conservation in Britain (38 pages); II. The present position and future prospects (32 pages); III. The future direction of Nature Conservation (32 pages). The last part is separately issued as the 15-page booklet mentioned above.

Future strategy is discussed under ten themes: 1. Give permanent protection to all sites specially important to nature conservation; 2. Conserve nature in the country as a whole; 3. Do more for marine nature conservation; 4. Extend and improve research and the availability of its results; 5. Increase public involvement and awareness; 6. Make conservation law work; 7. Develop Britain's role in international conservation; 8. Re-create habitats and re-introduce appropriate species; 9. Obtain increases in money and manpower; 10. Co-ordinate all efforts in nature conservation, particularly the interface between wildlife and geological conservation, on the one hand, and scenic and countryside amenity, on the other.

Throughout, clear guidance has been given to the conservation bodies (which include the B.S.B.I. – in part at least) as to the role they should be playing. The Society can help particularly in national surveys; by monitoring (and reporting) changes in S.S.S.I.s; in dissemination of information (especially through more popular publications on nature conservation); in promoting ecological studies by providing the taxonomic infrastructure and identification manuals; and in general by giving specialist expertise in vascular plant botany to Naturalists' Trusts, County Councils and other local bodies, water authorities, and the major national societies and associations involved in nature conservation.

William Wilkinson, Chairman of the N.C.C., said in his Preface: "We seek the support of the scientific world, whose researches are so important in determining the measures appropriate and necessary for the future. We wish to enlist the help of all caring people . . .". From recent developments within the Society's Council, it is clear that the B.S.B.I. has a role to play here and supports the Strategy. I hope that the majority of our members will read this book and face the challenge of putting these recommendations into effect.

A. C. JERMY

A concise Flora of Dorset. R. Good, edited by H. J. M. Bowen. Pp. xi+226 with 3 maps. Dorset Natural History and Archaeological Society, Dorchester. 1984. Price £4·50 including postage. Available from the Dorset County Museum, High West Street, Dorchester DT1 1XA.

Dorset is an attractive south-western English county bordering on the English Channel, predominantly agricultural but with some interesting heathland and tourist areas around Bournemouth, Swanage and Weymouth. It possesses a rich and varied flora, but despite being visited by botanists for over four centuries its botanical literature is curiously scanty. Nevertheless it has a distinction possessed by few other counties – three Floras and a handbook. The first Flora appeared in 1874, a second edition in 1895, the *Geographical Handbook* in 1948 and the work under review in 1984.

A concise Flora of Dorset is based largely on data accumulated by Professor Ronald Good, Emeritus Professor of Botany in the University of Hull, with a particular emphasis on his extensive botanical survey of selected areas of the county made between 1931 and 1939. The author's manuscript has, however, been edited, amended and added to by Humphrey Bowen, who also saw it through the press. The book is arranged in the manner of the traditional county Flora modified to the now sadly familiar truncated format utilized to keep down printing and publishing costs. The scientific nomenclature follows that of Clapham, Tutin & Warburg, *Flora of the British Isles*, 2nd ed. (1962), amended as necessary in line with the nomenclature of Tutin *et al.*, *Flora Europaea*, vols 1–5 (1964–1980) and Clapham, Tutin & Warburg, *Excursion Flora of the British Isles*, 3rd ed. (1981), while English names follow Dony, Perring & Rob, *English Names of Wild Flowers* (1980).

Apart from habitat and frequency data, locations are given for less common species. The assumed status of the many species is provided, but I find it difficult to accept *Fuchsia magellanica, Buddleja davidii, Symphytum orientale* and a host of other aliens as denizens. Certainly, the author defines his "denizens" as "plants which have been introduced by man intentionally and planted, some of these are now so well established as to have all the appearance of true natives". The generally accepted definition of a denizen as laid down by H. C. Watson over a century ago, however, is "a species at present maintaining its habitats as if a native without the aid of man, yet liable to some suspicion originally of having been introduced". Even if one accepts the present writer's definition of the term, *Buddleja davidii* and *Symphytum orientale* have spread from cultivated plants into the wild by seed, as have doubtless many other introduced species.

I find it difficult also to regard *Epilobium angustifolium*, *Senecio squalidus* and *Elodea canadensis* as "well-established casuals", while to describe *Simethis planifolia* (which occurred at Branksome from 1847 to c.1925) as "strictly a persistent casual" verges on the ludicrous.

A pleasing feature of the book is the citation of literary references against many of the records; less useful, sometimes misleading and often incorrect is the inclusion of many trivial, sometimes wrongly cited and often worthless varieties, mostly from the *B.E.C. Reports* of the Drucean era and from the *Journal of Botany* of the same period.

Errors are few, but *Rorippa islandica* (Oeder) Borbás (page 24) does not occur in southern England, the species intended being *R. palustris* (L.) Besser, ONOGRACEAE (p. 79) should read ONAGRACEAE and *P.×brunonianum* F. Schultz (p. 95) is *P.×braunianum* (F. Schultz) F. Schultz.

Up-dated accounts of the flora of the British Isles are essential to the study of the floristics of these islands, and Professor Good and Dr Bowen are to be congratulated on producing a detailed and accurate inventory of the modern flora of Dorset.

D. H. KENT

Nature's second kingdom. Explanations of vegetality in the eighteenth century. François Delaporte, translated by Arthur Goldhammer. Pp. xii+266, with 7 b. & w. text-figures. M.I.T. Press, Cambridge, Mass. and London. 1984. Price £7·55 (paperback edition; ISBN 0–262–54040–1).

Why do botanists think in the way they do? What are the paradigms of the subject as we now know it? Delaporte's *Le Seconde Règne de la nature* sets out to show that botany made little progress until the early seventeenth century and that the real advance took place in the eighteenth, when the essential framework of the subject was formed. The book is divided into four sections: 'The central problems of botany', 'Nutrition', 'Generation' and 'Movement'. These are prefaced by an Introduction and followed by a Conclusion, an Appendix (from Richard Bradley's *A philosophical account of the works of nature*, 1721, 1739), copious notes, splendid bibliography, a useful biographical glossary and an index of names.

Malpighi considered that the study of 'lower' forms of life would shed light on the workings of the 'higher'. Delaporte argues that it was in fact the reverse process that took place in that animals were used as the models for an understanding of plants. So plants still have veins. It may go further in that an understanding of animals has come from a knowledge of man in the egocentric thinking of a species put firmly in the centre of, and in complete mastery of, the world in the Judaeo-Christian tradition. Moreover, from Theophrastus onwards and most notably in Cesalpino, an understanding of plant function is indeed derived by analogy with that of animal physiology. It was not clear what the various bits of the plants did, but the plants functioned as living things and so models were sought in the animal world, where functions and bits could be linked. Contrariwise, some external parts of plants were readily visible and characteristic of particular taxa such that classification was more firmly established in botany than zoology, which used plants as the model in taxonomy. In nutrition, the mechanists looked for animal equivalents whereas Hales held that the roots absorbed nutrients and that sap was a progressive rather than a circulatory substance: if there was an animal-like circulation then there would be a need for only a little uptake of material whereas there was great uptake. The questions then revolved around whether the nutrients were ready-made or selected out or whether they were the same for all plants. Then there was the problem of life in that man was alive – an animal with internal sensations and therefore a soul, and animals were alive – plants with sensitivity and locomotion. Was life, the transformation of food into the creature's own substance, a property of matter or was there a vitalism, a 'soul' to be sought, perhaps in the pith of plants?

Goldhammer's translation is a valuable contribution to an understanding of the philosophical bases of botany, though perhaps it follows the rather circumlocutionary French a little too closely sometimes. What would be good now would be an investigation of how these bases restrict further development in the subject now. The mess that is the study of plant 'hormones' surely stems from an attempted analogy with animal hormones: the tens of thousands of pounds that have been expended in the search for 'florigen' bear witness to it. Again, the grip of the Neo-Darwinists on the study of evolution is largely a zoological one; but it is interesting that zoologists, in breaking free from that grip, have not turned to the findings of botany but to palaeontology as a model. Botany, the very word is almost a music-hall joke, needs to re-assert itself, and some hard thinking rather than chasing animal analogues must be the correct course. Thank you M. Delaporte.

D. J. MABBERLEY

The Macmillan Guide to Britain's Nature Reserves. Edited and partly written by J. Hywell-Davies & V. Thom. Pp. 717, with numerous colour and b. & w. photographs and coloured maps. Macmillan, London. 1984. Price £30·00 (ISBN 0–333–35398–6).

Any number of books exist to enable the armchair reader to imagine himself at some historic landmark or find his way there. The natural heritage has not been so well signposted. Here at last is a guide which takes the naturalist on a tour of Britain's wildlife, as displayed at nearly 2000 nature reserves and other sites; these cover the range of botanical meccas from the Avon Gorge to Yockletts Bank in Kent.

This book has the feel of a Whittaker or Who's Who and is the size of a dictionary, a substantial reference yet with a highly readable text. The introductory sections are kept to a minimum, and most of the space is given to descriptions of nature reserves and trails in each of the new counties of England and Wales and Regions of Scotland. A volume covering Ireland is promised. The character of each county or region is described by a local naturalist, sometimes a B.S.B.I. member. A map shows the location of those sites to which the public has access in the context of the county's essential features. The text describes a greater number of sites; for instance in Somerset and Avon the map shows 36 sites while 74 are described. The text is generously illustrated by well-reproduced colour and black & white photographs.

Each site entry gives a six-figure grid reference or, where this is absent, an indication of access arrangements, the size of area, the controlling body, habitat type and guidance to the best time of year for a visit. The length of description varies from four lines to several columns, the fullest being for National Nature Reserves and well-known Nature Conservation Trust reserves.

Never before has information relating to reserves under the control of different bodies been presented in one reference source. Under Somerset and Avon for instance, 30 Somerset Trust Reserves, 12 Avon Trust Reserves, 5 National Nature Reserves, 1 R.S.P.B. reserve, 4 private reserves, trails, a National Park and National-Trust-owned sites are described. The result is information on some of the best examples of British habitats presented side by side with that on sites of really very local interest or simply 'areas open to the public'. The Nature Conservation Trusts have, understandably, not put forward their best sites for inclusion in this volume. It is hoped that this book will convince some trusts that they can afford to be more generous over public access. This mixture does allow a range of sites, humble and first class of different kinds in any county, to be visited.

What does the book offer the botanist? Does it help him or her to explore the British flora, select and visit different habitats, even seek out some of the specialized or rarer species; and could it become a valued reference source? As the main habitat of each site is given, the book goes some way towards enabling anyone to see characteristic communities. The species index can guide one to examples of woodland dominated by alder, pine or birch or to heathland or mire. This same index also reveals localities of habitat-indicator species such as Yellow Archangel, Bogbean, Crested Buckler Fern, although the locations of our rarer wildflowers are not revealed. The combination of broad-brush descriptions of counties and detailed accounts of sites, presented in a handsome, richly illustrated format, should make this book a valued source of information.

The Guide sets out to be comprehensive, but it is by no means definitive. In a disarming way, the introduction refers to inevitable omissions and errors in what is recognized as being only a first attempt. In spite of these and the high price, Macmillan can be proud of a publishing achievement which should justify their confidence in the worth of the initial idea. After so many guides to the identification of species, this one may prove an important benchmark for public interest in wildlife places.

J. & J. ROBERTSON

The Kew Magazine, Vol. 1 Part 1. Edited by C. Grey-Wilson. Pp. 48, with colour frontispiece, six colour plates and numerous text illustrations and maps. The Bentham-Moxon Trust, Royal Botanic Gardens, Kew in association with Collingridge Books, Feltham, Middlesex. 1984. Price per volume (4 parts) £35·00 (ISSN 0265–3842).

This new quarterly journal is subtitled "Incorporating *Curtis's Botanical Magazine*" and includes six Plant Portraits of the sort that have made that publication a botanical and horticultural treasure house for almost 200 years. In addition, however, there are articles on 'The conservation of rare and endangered bulbs', 'Alpine ecology in the Barum Khola, Nepal', '*Lilium pyrenaicum* – a diverse species' and 'Portrait of a botanical artist, 1. Walker Hood Fitch', as well as 'Book reviews', 'Readers' letters' and 'Events of interest' (the 1984 Liverpool International Garden Festival and the 1985 Centennial Orchid Conference). The articles in future parts of *Kew Magazine*, we are told by the Director of Kew, Professor Arthur Bell, in a foreword, will be mainly concerned with conservation and ecology; but parts dealing with a single subject, as well as monographs of genera and groups of horticultural importance, will appear in an additional series.

The Kew Magazine is thus an expanded version of *Curtis's Botanical Magazine*, additional material consisting largely of features of more topical, less specialized interest than those that would normally appear in *Kew Bulletin*. The contributors to this first part all work at Kew or the Royal Botanic Garden, Edinburgh, and they maintain the high standard of botanical scholarship that one has come to expect in *Bot. Mag*. The emphasis is primarily horticultural, and B.S.B.I. members will not find much of immediate concern to the British or Irish floras in this part; but Christabel King's portrait of W. H. Fitch will fill in some interesting details of the life and work of a very fine botanical artist for those to whom he is known only as the joint (but major) 'author' with W. G. Smith of *Illustrations of the British flora*.

N. K. B. Robson

The sex life of flowers. B. Meeuse & S. Morris. Pp. 152, with 78 colour photographs, many line-drawings and several monochrome photographs. Faber & Faber, London & Boston. 1984. Price £12·50 (ISBN 0–571–11909–3).

This book is about the adaptations shown by flowers in relation to pollination. The greatest variety of such adaptation is expressed in relation to animal pollination, and accordingly the book, though plant-orientated, is also about the animals concerned: several orders of insects, several families of birds, various bats, and some non-flying mammals, both marsupial and placental. The account is introduced by a survey of life-cycles in the main classes of lower plants which shows how the reproductive system of Angiosperms evolved. The text is designed to be understood by readers without prior knowledge; I think that the links in the chain of thought are occasionally too weak to carry the complete novice to full understanding, but on the whole the story is told with outstanding clarity, and the book is highly recommended for the amateur. 'Telling a story' gives a clue to the style of writing; it is 'chatty', not 'text-book', but this should not deter sixth form scholars and university students, who will get a very good introduction to the science of pollination-biology from this book. It is in the book's favour that a moderate amount of technical terminology is introduced (always with explanation) and that scientific names are given for most organisms. Although some relevant aspects of the ecology of flowers and their pollinators are scarcely touched on, the book includes a – to me, mouth-watering – bibliography which will lead the researcher into every corner of the field.

Leaving aside a few possible criticisms which, in a book on this level, could be treated as quibbles, I feel that the authors have been so keen to cover the more remarkable flower/pollinator interactions that they have not given enough weight to the more usual relationships. A more specific complaint is that some flowers that deceive insects are dealt with in the chapter called "The 'unacceptable' face of pollination", whereas others, the 'mushroom-gnat' flowers, are dealt with under "Adaptation and co-evolution"; it is left to the reader to notice that the same principle is involved. The same goes for figs and yuccas, which are separated because they are pollinated by different orders of insects.

It is, however, good to find all the biologically more exciting pollination systems covered. Some of these have long been known, others recently discovered. Few have been photographed before, and here now we have absolutely splendid colour photographs of the familiar flowers and the bizarre, and of their pollinators; the subjects range from the hoverfly on an 'umbel' to a terrestrial rodent manipulating a ground-level *Protea* head, a pollination relationship that was first described only in 1978. These photographs were mostly taken by the staff of Oxford Scientific Films (including Sean Morris) in the course of work on the TV film 'Sexual Encounters of the Floral Kind'.

This book is attractive, scientifically sound and up-to-date, and enjoyable to read.

P. F. Yeo

Watsonia, **15**, 417–419 (1985)

Obituaries

WILLIAM ANDREW CLARK
(1911—1983)

Dr William Clark died on 19th November, 1983 at his home in Ryton, Tyne and Wear, aged 72. In him the B.S.B.I. has lost one of its longest-standing members, his membership extending over 46 years.

He was born in Girvan, Ayrshire, and after some moves the family finally settled in Dundee. It was at the University College there (now the University of Dundee) that William embarked upon a botanical career. After graduating he stayed on to carry out research for which he gained a Ph.D. in 1936. Apart from a few months spent as an Assistant Lecturer at Liverpool University he spent the whole of his professional life in the Department of Botany (now Plant Biology) at Armstrong College, later to be known as King's College and finally as the University of Newcastle upon Tyne. For many years he not only lectured in the Department but also played an important role in the life of the University as Senior Tutor in Science.

William Clark's interest in alpine and mountain floras was undoubtedly stimulated by his love of hill walking and climbing, at which he was indefatigable. These attributes made him an invaluable member of the Newcastle group carrying out detailed investigations into the flora of the Inner and Outer Hebrides and its origins. Many of the plant records obtained were the result of his skill in spotting the plants in seemingly inaccessible places and in ultimately reaching them, often by dangerous routes. This interest in alpines spilled over into his hobby of gardening, his pans of beautifully grown plants winning many prizes at both local and national level.

William Clark's knowledge of the flora of north-eastern England was unrivalled, and he did much to stimulate a wider interest in the botany of the area. As a consequence he was in great demand as leader of field meetings of the Natural History Society of Northumbria, and his University field courses introduced many generations of students to the beauties of the Northumbrian scenery and flora. Many records were contributed by him to the *Atlas of the British Flora*. Conservation was a subject dear to his heart, and he was a founder member of the Northumberland and Durham Naturalists' Trust and of the Northumberland Wildlife Trust. His advice was sought in such matters as the protection of the Cow Green reservoir site in Upper Teesdale and in the selection of S.S.S.I.s. William was a very forthright person whose absolute integrity made his advice so valuable.

William Clark predeceased by only two months his wife Helena Heslop Clark (known universally as Dolly) who was the daughter of Professor J. W. Heslop Harrison, F.R.S. and grand-niece of the Rev. J. E. Hull, another outstanding north-eastern naturalist. They leave a daughter, to whom our sympathy goes.

T. G. Walker

RICHARD CREWDSON LEAVER HOWITT
(1911—1984)

A unique era of Nottinghamshire plant recording ended on 19th June 1984 with the tragic death of Leaver Howitt. Since he became B.S.B.I. recorder for v.c. 56, botanists have much enjoyed his individual approach, his characteristic forthright manner and above all his enthusiasm. Jointly with his wife Brenda, also a very competent botanist, who shared with him his love of the countryside and profound interest in plants, every inch of his native county was searched during their survey to produce the 1963 *Flora of Nottinghamshire*.

Leaver was not a computer-based botanist, but a field naturalist and plantsman of a past era, unbelievably unorthodox, but most concerned with recording, parish by parish, the four divisions of the county on which his *Flora* is based.

Leaver and Brenda Howitt were a team combination of great intellect and scholarship. Brenda had unparalleled charm and a quiet dignity which contrasted sharply with Leaver's boisterous nature. Consequently B.S.B.I. and W.F.S. excursions, of which there were many hosted by the Howitts, were a combination of hard work and humour, and always fun.

Leaver was an acknowledged authority on and B.S.B.I. referee, together with R. D. Meikle, for the Salicaceae and, with A. C. Jermy, for the Potamogetons. While he was the Notts. County Recorder and Brenda was the Branch G Secretary for W.F.S. (from 1955), in truth all tasks were shared. This characterized the whole of their activities and life together; as P. C. and J. F. Hall in an obituary to Brenda stated, they were "a partnership which delighted all who encountered it".

Leaver Howitt was born on 16th July 1911 at Farndon, the only child of Richard Holmes Howitt, gentleman and Ellen Beatrice Howitt. He lived there all his life, taking a great interest in the village, its church and its people. He spent some time at Malvern Boys College. In 1949 he joined the B.S.B.I.; in 1950 he met Brenda Chalk, and they were married in 1951.

Leaver Howitt's ambition to succeed in writing a Nottinghamshire *Flora* was realized in 1963 after twelve years of recording. The last previously published *Flora* of the county was also by a Howitt – his great-great-uncle Godfrey, who published a small volume in 1839 before emigrating to Melbourne. Between this and the present Howitt *Flora*, a manuscript *Flora* was written by Professor Carr; but it was never published, so that the *Flora of Nottinghamshire* (1963) by R. C. L. and B. M. Howitt succeeds those of Dr Charles Deering (1738), Thomas Ordoyno (1807) and Dr Godfrey Howitt (1839).

In 1961 Leaver and Brenda discovered a strange *Calystegia* growing outside the ambulance station on Queen's Road, Newark. This was recognized at Kew as a new interspecific hybrid and named subsequently in 1980 *Calystegia*×*howittiorum* Brummitt. It is known only from Nottinghamshire and Scarborough, Yorkshire (v.c. 62). The genus *Howittia* is also associated with the family, the generic name being given to a mallow in honour of Godfrey Howitt (1856).

From 1954 to 1960 the Howitts recorded in all the 10 km squares in the county for the *Atlas of the British Flora* – members of a select band which achieved this almost unassisted. Without them, Nottinghamshire would almost certainly have been under-recorded; with them, it was one of the best covered counties of the Kingdom. But they were no stay-at-homes and, along with the Donys and the Halls, were one of the couples who seemed to attend almost all the mapping weekend and week meetings. From Cornwall to Coldstream, Llandrindod Wells to Bury St Edmunds they came in their elegant and venerable Rolls, returning home early only once, defeated by mice in a hotel bedroom at Duns. They also gave particular help in Lincolnshire to their great friend Miss E. J. Gibbons, concentrating on Lincs./Notts. border squares and others in S. Lincs. (v.c. 53).

After the publication of their *Flora*, they botanized further afield – northern Norway, Iceland and Greenland. They accumulated many records for the Tromsö Museum in Norway, and Leaver made a large herbarium of northern plants. Whereas their interest in willows prompted the Arctic adventures, their interest in daffodils led them to the Scillies. Leaver grew a superb collection of daffodils which he propagated extensively and sold with many other treasures at the 'Farndon Open Days'. These were held in aid of the County Trust for Nature Conservation, with which he was closely associated.

Leaver was primarily a plantsman and a very active gardener. His large garden enabled him to pursue an interest in horticultural conservation and collect some of the earlier varieties of herbaceous plants not readily available today; he also collected unusual shrubs. His was essentially a botanist's garden, growing 'curiosities', weeds now extinct in the county, and some of the 'difficult' plants, which were much appreciated by newcomers to recording. The garden at Farndon, alongside the Trent water meadows, also extended into the famous Willow Holt, where many were initiated into the mysteries of the *Salix* hybrids. prompting the writing of a series of willow identification articles (another joint effort) for the W.F.S. magazines in 1977. Leaver also published *A study of the Attenborough Nature Reserve* – perhaps a consequence of his long involvement with the Trent Bird Watchers. His other interests included early agricultural equipment, traction engines and vintage cars, as well as antiquarian books, an interest that he maintained up to the time of his death, researching sources for himself and his friends.

With the untimely death of Brenda in 1981, Leaver's world fell apart. His own health was failing, his illness being very painful, at times depressing and, as he was sadly aware, incurable.

Leaver Howitt's enthusiasm for plants was infectious. His correspondence was literally voluminous, most of his letters being written on the backs of the covers of company reports as thick as the file they rapidly filled. His records are a delight to read, amusing, with local anecdotes far too numerous ever for publication, but instilling into the reader the enjoyment which he and Brenda transferred to all of us who had the privilege of knowing them and botanizing with them.

The herbarium of Leaver Howitt has been given to the University of Cambridge (**CGE**) and his manuscripts and records to the Notts. County Records Office.

I. Weston & F. H. Perring

MAYBUD SHERWOOD CAMPBELL

A correction to her obituary (*Watsonia* **15**: 157–160 (1984))

From David Allen, I have learned that Maybud was christened May. She became known to her family as Maybud to distinguish her from her mother, who was also May, and this nursery nickname stayed with her for the 79 years of her life.

E. Milne-Redhead

Reports

CONFERENCE REPORT

ARCHAEOLOGY AND THE FLORA OF THE BRITISH ISLES

Some 120 members of the Association for Environmental Archaeology and the B.S.B.I. (about 50% B.S.B.I. members, but some members of both societies) gathered at St Anne's College, Oxford from 21st to 23rd September 1984. The conference presented topics of mutual interest and the weekend was a vehicle for much enthusiastic and stimulating discussion between botanists and archaeologists. The programme was divided into six sections, which considered respectively aspects of the history of woodlands, grasslands, moorlands, coastlines, and arable and ruderal weed communities in Britain. It should be noted that, although the meeting was billed as concerning the "British Isles", practically no mention was made of Ireland.

Since the Mesolithic period there has been a progressive clearance by man of our native forests by burning, cutting and grazing of animals. These processes have interacted with episodes of climatic deterioration and amelioration and probably diseases, such as the Dutch Elm Disease that has so recently decimated our elms and changed the landscape of England. Clearing of forests had an effect on soils and on the runoff of water, with consequent influence on sedimentation patterns. The development of agriculture gave rise to a whole number of environmental changes, not least the evolution of a weed flora by recruitment of native, opportunist species, together with an adventive element transported by human agency. New ecosystems gave these weeds huge potential success, a process that continues to the present day. The story was brought to life on the Saturday afternoon by excursions to Port Meadow, a vivid link with medieval Oxford life, and to Shotover Wood. The papers presented, despite their variety of content, served to indicate the importance of ancient ecological events and processes for a full understanding of our contemporary flora and vegetation, whilst at the same time emphasizing that the geologists' principle that 'the present is the key to the past' is necessary for the interpretation of the historical/archaeological record. Archaeological studies, frequently based on the investigation of fragmentary or damaged samples of plant or animal remains, particularly stress the importance of distinguishing hypothesis from evidence in ecological or floristic research. One is mindful of the recent comments of Professor D. A. Webb (*Watsonia* **15**, p. 233 (1985)) – "We must recognize that nearly all their macroscopic material is of a kind that the normal taxonomist would reject as totally inadequate for identification". Thus, our joint meeting, with vigorous discussion and extensive contacts between those who study floras and those who study the remains of floras, will have been most valuable. A full text of the papers delivered will be published in due course by the A.E.A.

J. R. AKEROYD

EXHIBITION MEETING, 1984

The Annual Exhibition Meeting was held in the Department of Botany, British Museum (Natural History), London, on Saturday, 24th November 1984, from 12.00 to 17.30 hours. The following exhibits were shown.

TOWARDS A REVISION OF *FLORA EUROPAEA*, VOLUME I

Flora Europaea Volume 1 (1964) is currently being revised at Reading University. During the 20 years since this volume appeared, there has been considerable taxonomic and floristic activity in

Europe. New species and subspecies have been described in the European flora, new nomenclatural combinations have been made, species have been noted as new to Europe (although already known outside the continent) or European taxa have been found to be the same as taxa found in other parts of the world and many adventives have been noted as newly naturalized or overlooked. Taxonomy has flourished in previously relatively poorly known parts of southern Europe (areas with rich floras) and there has been a veritable flood of discovery and publication. The scientific literature in our field has expanded hugely. A good deal of this vigour and consequent build-up of new data is a direct consequence of the publication of *Flora Europaea*.

Therefore, Volume 1 is currently being revised on a grant from the Linnean Society *Flora Europaea* Trust Fund. The exhibit demonstrated aspects of the revision of *Silene*, the largest genus in Volume 1, which requires several new text entries together with many minor but essential changes in the descriptions, geographical data and chromosome numbers. It is envisaged that the revised volume will incorporate about a 10% increase in text and that the revision will take five years to complete.

J. R. AKEROYD

SOME TETRAPLOID REYNOUTRIAS

A recent survey of the chromosome numbers of *Reynoutria japonica* Houtt. in the British Isles revealed the great majority to be octoploid ($2n=88$). Plants from clones at South Wylam, Co. Durham (v.c. 66), Gomshall, Surrey (v.c 17), and Cirencester, Gloucs. (v.c. 33), were, however, tetraploid ($2n=44$). Whilst superficially similar to *R. japonica*, these plants bore a close resemblance in habit and morphology to plants from some reciprocal crosses between *R. japonica* var. *compacta* (Hook. fil.) Buchheim and *R. sachalinensis* (F. S. Petrop.) Nakai produced at Leicester ($2n=44$). Closer examination revealed the leaves of both groups of plants to be of intermediate size and shape between *R. japonica* var. *compacta* and *R. sachalinensis*; and that cuticular and trichome (hair) type were either intermediate or derived from one parent, and were in marked contrast to the leaves of the octoploid *R. japonica*.

Furthermore, the good seed-set on one of the artificial hybrids and on the Gomshall plant suggests a close relationship between *R. japonica* var. *compacta* and *R. sachalinensis*.

J. P. BAILEY & A. P. CONOLLY

PELORIA AND PSEUDOPELORIA IN BRITISH ORCHIDS

Although all our native orchids have bilaterally symmetrical flowers, rare peloric mutants develop radial symmetry, either by the replacement of the inner perianth segments with two additional labella or by replacement of the labellum with a third, undifferentiated, inner perianth segment. Pseudopeloric orchids, which are more common but less frequently recorded, have labella that are similar, but not identical, to the outer perianth segments. They have often been misidentified as peloric specimens or as hybrids, e.g. the supposed intergeneric hybrid×*Pseudanthera breadalbanensis* McKean (*Pseudorchis albida*×*Platanthera chlorantha*). Peloric and pseudopeloric individuals of several species were illustrated, and their significance discussed.

R. M. BATEMAN

FARMING AND WILDLIFE (FWAG) IN SOMERSET

63 counties in Britain have a Farming and Wildlife Advisory Group (FWAG), a voluntary representation from those organizations relating directly to farming and conservation. Through the formation of the Farming and Wildlife Trust, ten counties now have full time Farm Wildlife

Advisers. The trust hopes to raise enough funds both nationally and locally to appoint another thirty.

There has been a growing awareness by both the general public and the farming community that the conservation of wildlife is an aspect of farming that should be duly considered, having suffered particularly through lack of attention concurrent with changing farm practices over the past forty years.

In order to help farmers and landowners who would like some advice on whether they can do anything (however small) towards increasing or maintaining a wildlife interest on the farm, Advisers are needed on the ground – readily contactable, able to give general advice, co-ordinate specialist advice, provide information on grants available, and encourage interest and understanding.

Examples of the type of work, by means of a photographic display, leaflets and notes, were exhibited from the county of Somerset.

J. BERESFORD

ARMERIA MARITIMA SUBSP. *HALLERI* (WALLR.) ROTHM.

Armeria maritima subsp. *halleri* (Wallr.) Rothm. is recorded from serpentine and heavy-metal-rich soils in western Europe. A plant resembling this taxon occurs on copper mine spoil in North Wales, but has no clear features to distinguish it from subsp. *maritima*. In Britain, subsp. *maritima* has leaves which are always hairy or ciliate and also hairy scapes, while subsp. *elongata* has hairless scapes. The Welsh plant is best regarded as an ecotype of a very polymorphic species.

H. J. M. BOWEN

FILAGO PYRAMIDATA L. REFOUND IN WEST SUSSEX (V.C. 13)

F. pyramidata L. (*F. spathulata* C. Presl) was last recorded in West Sussex in 1905. In the summer of 1983 it was found in Halnaker chalk-pit by H. W. Matcham, and again in 1984 when many hundreds of very small (up to 1·25 cm) plants were growing on the floor of the pit. *F. pyramidata* had been collected from this site by H. L. F. Guermonprez in 1891 and one of his herbarium sheets and his painting of the plant – on loan from the Portsmouth City Museums – together with specimens and photographs from the site in 1983 and 1984 were exhibited.

M. BRIGGS & H. W. MATCHAM

THE INTERPRETATION OF PLANT MACROREMAINS IN ARCHAEOLOGY

Archaeobotany is concerned with the interaction of man and plants in the past. It involves:

a) reference to collections of modern comparative plant material to obtain a detailed knowledge of anatomy for the identification of plant tissues that may be small and altered fragments;
b) an understanding of present-day phytoeceological systems of wild plants as well as weeds and crops;
c) a study of ethnobotany;
d) the use of ethnographic models of agriculture and food-processing technologies, derived from recorded observations and collections in the field.

Assemblages of plant macroremains in archaeological deposits may include components from the surrounding wild flora, weeds, wild plants gathered and brought into the site by man, the products and by-products of cultivation, or admixtures of any of these.

"Interpretation may go far beyond the obvious and immediate significance of the food plants, and comparative studies of different periods or geographical areas can build up a corpus of knowledge about plant geography and ecology" (G. W. Dimbleby, *Plants and Archaeology*, 2nd ed. London. 1978, p. 12.).

A. Butler, J. Fitt & M. Nesbitt

ARCTIC-ALPINES OF BRITAIN AND THE NORTH-WEST HIMALAYA

When visiting the western end of the Himalaya it comes as quite a surprise to encounter a number of species that also occur in the mountains of Britain. The following species were observed during the Kashmir Botanical Expedition 1983 or the Southampton University Ladakh Expedition 1980: *Asplenium septentrionale* subsp. *septentrionale*, common from 2400 m to the snow-line; *Asplenium viride*, common at high levels, 2750–4250 m; *Carex microglochin*, common in wet places on alpine meadows, 3350–5200 m; *Cerastium cerastioides*, found almost everywhere; *Galium boreale*, common in temperate and alpine zone, 1500–4000 m; *Lloydia serotina*, widespread, 3350–5200 m; *Polygonum viviparum*, common in marshy places in the alpine zone, 2750–5200 m; *Polystichum lonchitis*, cosmopolitan high-level fern common in the birch zone, 2750–3650 m; *Rubus saxatilis*, 2750–4250 m; *Saxifraga cernua* f. *bulbillosa*, 3650–5200 m; *Thalictrum alpinum* var. *microphyllum*, very common amongst mosses and sedges on alpine meadows, 3650–4800m; *Veronica serpyllifolia* ssp. *humifusa*, very common, 2100–4000 m.

C. A. Chadwell

LLEYN – SOME 1984 RECORDS

Additions and new records from West Lleyn (Caerns., v.c. 49) during 1984 were mainly introduced species either naturalized garden outcasts or escapes. They included some six species of *Cotoneaster*: as well as the more usual *C. horizontalis* and *C. simonsii*, *C. dielsianus* (Edeyrn Cemetery walltop), *C. franchetii* and *C.* × *watererii* group on waste-ground, probably bird-sown, and a black-fruited, planted, species (either *C. foveolatus* or *C. acutifolius*) with seedling progeny naturalizing. *Oenothera* × *fallax* (2 localities) and *Verbascum phlomoides* appeared on waste-ground or rubbish dumps; *Symphytum tuberosum* and a *Helichrysum* were established away from houses following presumed garden jettisoning. Several of these have no or few recent records from North Wales. A wild rose, probably *R. obtusifolia*, has also not apparently been recently recorded from North Wales.

A. P. Conolly

BRITISH VARIANTS OF THE BEE ORCHID

The high frequency of autogamy (self-pollination) in British Bee Orchids (*Ophrys apifera* Hudson) enables morphological variants arising through mutation to persist and sometimes predominate at certain localities. Photographs of the two most striking variants that occur in Britain were shown in this exhibit. *O. apifera* var. *trolli*, the 'Wasp' Orchid, with an unrecurved tapering lip bearing diffuse yellow and brown markings, is now rare and virtually restricted to south-western England. *O. apifera* var. *chlorantha*, an apigmentose variant with pure white sepals and a yellow-green lip, is very locally frequent in East Suffolk. A provisional distribution map for these two varieties was displayed and additional records for either taxon were requested.

I. Denholm & B. Denholm

SOME INLAND OCCURRENCES OF COASTAL SPECIES IN SOUTH LANCASHIRE

Industrial waste sites in Merseyside have in some cases been abandoned for more than 100 years. The long period over which recolonization has proceeded, and the peculiar soil conditions resulting from the weathering of the waste materials, has led to the development of some unusual assemblages of plants, including species normally restricted to coastal habitats in the region.

Some of the examples presented were seen during the field meeting in St Helens and Wigan on 28th & 29th July 1984. Waste sites included saline pools with water pumped from coal mines, colonized by *Scirpus maritimus*; sandy heaps made from the products of plate glass manufacture, with *Carex arenaria*, *Ammophila* and *Leymus*; pulverized fuel-ash tips from power station waste, with various species of *Dactylorhiza* and their hybrids; and one of the oldest types of chemical waste, the highly calcareous effluent from the Leblanc process, which supports species such as *Anacamptis pyramidalis*.

J. Edmondson

ZOSTERA OF THE SEVERN ESTUARY (V.C. 35)

All three *Zostera* species, *Z. marina* L., *Z. angustifolia* (Hornem.) Reichenb., *Z. noltii* Hornem., were confirmed by Prof. T. G. Tutin for v.c. 35. The material exhibited showed obvious *Z. marina* and *Z. noltii*. Studies of plants in the estuary from the beginning of September to the beginning of November revealed no obvious *Z. angustifolia*. This plant was first identified in August 1972 and confirmed by T. G. T. The turbulence of the estuary, due to a number of factors, prevents the normal development of *Z. marina* and no leaves of it have been seen to exceed 5 mm in width, few attain it, and the average width is less than 4 mm, even in non-flowering stems, The lengths of the inflorescences are very much below those quoted in NCC's "Guide to Identification of Difficult Plant Groups". Numerous plants, looking like *Z. angustifolia* in the field, proved to be *Z. marina*, on the basis of fruit and seed size. A soft, sticky mud-band, near the shore, makes access to the gravel beds and the eelgrass difficult and probably accounts for the plant's absence from the local Floras of Hamilton, Shoolbred and Wade.

T. G. Evans

IS THERE A DIFFERENCE? POPULATIONS OF *MUSCARI NEGLECTUM* GUSS. EX TEN.

Observations of flowering plants of *Muscari neglectum* Guss. ex Ten. (*M. racemosum* auct.) at Tuddenham Gallops (v.c. 26) and at Chadlington (v.c. 23) have suggested to me that there might be a varietal difference between these populations. The Suffolk plants all had a particularly dark, compact inflorescence, while those in Oxfordshire displayed a brighter colour and a more elongated inflorescence with the crowning sterile buds noticeably paler than the other flowers and forming an obvious 'tuft'. Photographs taken in 1982 and 1984 were displayed, together with herbarium material from East Anglia and Oxfordshire which also illustrated this apparent difference.

R. FitzGerald

HIERACIUM SPELUNCARUM ARV.-TOUV. AT RICHMOND HILL, BRISTOL

Photographs taken in 1984 were displayed with others of this hawkweed in the identical location, taken by H. S. Thompson in 1931. Other prints showed the plant "flowering handsomely" nearby, as described by J. W. White, in *The Bristol Flora* (1912). Close-ups of the glandular inflorescence were included, and a detail of dust sticking to the densely glandular upper surface of the leaves.

The latter character distinguishes the *Amplexicaulia* group (*H. amplexicaule* L., *H. pulmonaroides* Vill., and *H. speluncarum* Arv.-Touv.) from all other hawkweeds known in Britain and Ireland.

R. FitzGerald

BIOSYSTEMATIC STUDIES OF *PARNASSIA PALUSTRIS* L.

Experiments on the sand-dune ecodeme of *Parnassia palustris* L., known as var. *condensata* Travis & Wheldon, showed that a) it retains its dwarf, compact habit in cultivation, and b) it breeds true from seed. Its varietal status is therefore supported. Chromosome counts made on British material of var. *palustris* and var. *condensata* show that both taxa have diploid ($2n=2x=18$) and tetraploid ($2n=4x=36$) cytodemes. The tetraploids apparently have a more northerly distribution than the diploids.

R. J. Gornall

FIELD MEETING – LAUTERBRUNNEN, SWITZERLAND: 25TH JUNE–2ND JULY 1984

A selection of colour prints and transparencies of alpine plants and scenery by members of the party was exhibited, together with specimens of lichens collected by Mrs M. Hale and the preliminary draft of the Field Meeting Report for *Watsonia*.

A. L. Grenfell

CUCURBITACEAE IN BRITAIN

The draft of *Adventive News* **29** dealing with Cucurbitaceae in Britain and illustrated by G. M. S. Easy was shown, together with fruits of Bottle Gourd, *Lagenaria siceraria* (*L. vulgaris*); Cucumber, *Cucumis sativus*; Ornamental Gourds and Vegetable Marrow, *Cucurbita pepo*; Pumpkin, *C. maxima* and Vegetable Sponge, *Luffa aegyptica* (*L. cylindrica*). Herbarium sheets were shown of the rare wool alien *Cucumis myriocarpus*; the greenhouse curio *Cyclanthera brachystachya* (*C. explodens*), naturalized in a vegetable plot at Newbridge-on-Wye, Powys; Water Melon, *Cucumis melo*; Squirting Cucumber, *Ecballium elaterium* and Balsam Pear, *Momordica charantia*.

A. L. Grenfell & C. G. Hanson

ALIEN NEWS

Herbarium sheets were shown of the following legumes: *Astragalus hamosus, Trifolium hirtum, T. lappaceum, T. nigrescens, T. resupinatum, T. retusum, T. spumosum, T. suffocatum, T. tomentosum, Trigonella monspeliaca, Vicia narbonensis* and *V. villosa* subsp. *varia* (*V. dasycarpa*). These represent a selection of tan bark aliens found during 1984 at the Manor Tannery, Grampound, E. Cornwall (v.c. 2).

A. L. Grenfell & K. L. Spurgin

WOODLANDS IN NORTH LONDON – THEIR EDUCATIONAL VALUE

Within the boundaries of the London Borough of Haringey lie surviving fragments of the, once extensive, ancient Middlesex Wood. The nature and character of these isolated woods today is far removed from the 'natural' climax forest that once covered this area. Remnants of this forest are found in Highgate, Queens and Coldfall Woods. The character of each of these woods is also markedly different, the structural and botanical attributes reflecting the past history and current management practices in each area.

To encourage the use of these woodlands for teaching and ecological field-work, the Urban Spaces Scheme at The Polytechnic of North London has completed extensive and detailed field surveys and has devised work programmes and projects for both primary and secondary schools centred on these woods.

The exhibition display portrayed the ecology of these north London woods and showed how this information may be used for teaching purposes at all levels. Project work undertaken by the Scheme and teachers illustrates the educational value of these field-based programmes in ecology.

M. HALE

THE BOTANICAL ILLUSTRATIONS OF JAMES BRUCE'S TRAVELS TO ETHIOPIA C.1770

Although not strictly the province of the B.S.B.I. this exhibit was of general interest and related to the expedition of a famous Scottish traveller. James Bruce published his *Travels to discover the source of the Nile in the years 1768–1773* in 1790 in which were included 15 engravings of plants. The second (1805) and third (1813) editions added nine more plates. Very little was known at that time about the botany of tropical Africa. The artist Luigi Balugani, who died in 1772, made superb watercolours and sketches of 162 species which have been overlooked for some 200 years. They are owned by Lord Elgin and the Yale Center for British Art and will soon be published by A. A. Balkema, with text by F. Nigel Hepper, Ib Friis and Paul Hulton.

F. N. HEPPER

DISTRIBUTION OF TWO SPECIES OF *CHRYSOSPLENIUM* WITHIN A MIXED POPULATION ON A GLOUCESTERSHIRE NATURE RESERVE

Chrysosplenium oppositifolium and the less common *C. alternifolium* both occur in wooded stream margins. On the Snow's Farm Local Nature Reserve (Gloucestershire Trust for Nature Conservation) near the Cotswold village of Slad, they grow in mixed populations. Five transects, 1 m apart and 17 m long, extending at right angles from a stream up a slope, were sampled at 25 cm intervals by point quadrat (10 pins 5 cm apart at right angles to transects). In addition to the two species of *Chrysosplenium*, the cover of *Ranunculus ficaria* was also recorded.

The commoner *C. oppositifolium* was confined to the wettest part of the sample area, occupying flat land near the stream. *C. alternifolium* was found to be much more abundant than had been expected and although its centre of distribution was also in the wettest places it extended, albeit thinly, into drier parts of the transects, and thus was shown to have, at this site, a broader habitat range than the nationally commoner *C. oppositifolium*. *Ranunculus ficaria* was confined to the drier places, and was negatively correlated with both *Chrysosplenium* species, perhaps in relation to differences in available light intensity in the open woodland.

It seems that the two species overlap in their distribution but, it is suggested, they co-exist in similar ecological niches because the less robust one can tolerate a greater degree of moisture stress and hence maintain a diffuse population beyond the range of the other.

M. HICKEY, D. R. SLINGSBY, *ET AL.*

A FEW PROBLEMS IN *MOEHRINGIA* L. (CARYOPHYLLACEAE)

Moehringia L. is a genus of some 30 species distributed across much of Europe, with two species in North America, and one in Morocco. Several avenues of current research were illustrated, many of which have posed, and still do pose, some problems.

Only two wild hybrids have been described. The type locality of *M.* × *coronensis* Behrendsen from below the monastery of Madonna della Corona, Monte Baldo, Italy was illustrated. Pollination barriers have proved to be largely spacial rather than sexual. Many hybrid combinations have been created.

Studies of capsule walls and nectaries have either been overlooked or misinterpreted in the past. The Scanning Electron Microscope has proved to be a useful routine research tool in many ways. The pollen of *Moehringia* is stenopalynous. Species can be distinguished by using a limited number of characters, including grain diameter, and pore diameter and number. Seeds provide the most valuable character set for delimitation of taxa. The strophiole – seed appendage – of several species was illustrated to indicate its integumental origin.

A series of illustrations of *Moehringia trinervia* served to thank members who had replied to a *B.S.B.I. News* request. Cultivation experiments have shown that variation in taxa is due to local environmental conditions and the season of seed germination. Much of the variation indeed cannot be included within the normal parameters of subspecies.

D. J. N. Hind

PHOTOGRAPHS OF WILD FLOWERS FROM SOUTHERN ENGLAND

A collection of 13 volumes of photographs of flowering plants taken in the southern counties of England, from Dorset to Kent and northwards to include Oxfordshire was shown. The collection was started in 1982 as a hobby, but has since become a much more serious undertaking. As well as the exhibited photographs, detailed written records of sites where each species was found are being kept. The author expects to complete a further six or more volumes during 1985 and hopes to be able to exhibit these at future Annual Exhibition Meetings. The photographs, negatives and information about sites are available to interested parties.

V. A. Johnstone

TAXONOMY AT READING

This composite exhibit outlined some of the taxonomic work currently being undertaken in the Plant Science Laboratories, University of Reading:

- J. B. Harborne, Marian Boardley and H. P. Linder showed how in *Chondropetalum* (Restionaceae) phytochemistry has supported recent data from anatomical studies and has enabled H. P. Linder to revise the taxonomy of the genus.
- C. S. Williams, Jennifer H. Fronczyk, and J. B. Harborne demonstrated the use of leaf flavonoids as indicators of parentage in some *Fuchsia* hybrids. The flavonoid profile of *Fuchsia* 'Mary' is a clear addition of those of the two suspected parents and identical to the synthesized hybrid.
- S. Z. Husain exhibited variation in morphological, palynological and phytochemical features of species of the genus *Origanum* L.
- W. E. Eddie outlined the progress made so far in the development of the P. S. L. Botanic Garden in Whiteknights, and the plans for a national conservation collection of *Iris* species and a proposed replicate of Linnaeus' garden in Uppsala.
- D. J. Farmer and S. L. Jury displayed the production of computer printed labels for and lists of herbarium specimens, and explained how the system enabled collections to be speedily and efficiently processed for incorporation and distribution.
- Other exhibits relating to work at Reading were those of J. R. Akeroyd (*Flora Europaea* revision) and D. J. N. Hind (*Moehringia*).

S. L. Jury

HELP!

This regular exhibit offers informal help with the identification of awkward specimens, by inviting all visitors to the exhibtion to make suggestions as to their identity. 30 plants from various sources were shown, and helpful suggestions were made for most of them. Species named included *Abutilon theophrasti* Medicus, *Setaria* species and three samples of *Lemna minuscula* Herter.

S. L. M. KARLEY

ORCHIS FRANCIS-DRUCEI AND *DACTYLORHIZA INCARNATA* SUBSP. *CRUENTA* IN WEST ROSS (V.C. 105)

Orchis francis-drucei was described as a new species of orchid by A. J. Wilmott from a small colony above Loch Maree, discovered whilst on an excursion with G. C. Druce in 1935. Since the original discovery, the plants apparently remained undetected until a colony of similar plants was found near Loch Maree by M. R. L. in 1983. A study of this colony by the authors in 1984 has demonstrated that both the 1935 and 1984 colonies are referable to *Dactylorhiza traunsteineri* (Sauter) Soó. Photographs and details of the 1984 colony were displayed together with Wilmott's description. The Loch Maree record re-establishes *D. traunsteineri* as a Scottish plant following the deletion of the Knapdale records (*Watsonia* **14**: 415–417, 1983).

D. incarnata subsp. *cruenta* (O. F. Mueller) P. D. Sell was first discovered in Scotland from West Ross in 1982 and reported in *Watsonia* **15**: 11–14 (1984). Photographs of the plant were displayed.

M. R. LOWE, D. J. TENNANT & A. G. KENNETH

THE GUERNSEY BAILIWICK 1984

Specimens were exhibited of some of the good finds of the year: viz. *Equisetum* × *litorale* and *Allium subhirsutum* (from Sark) new to the Channel Islands; *Viola tricolor*, first confirmed record for Sark; *Sinapis alba*, only other record 1908 (sans specimen); *Rubus idaeus*, new to Sark; *Pyrus pyraster*, new to the bailiwick; *Polygonum oxyspermum* subsp. *raii* on Guernsey, thought lost to the bailiwick; and *Puccinellia distans*, second confirmed record for the bailiwick this century.

J. PAGE

PLANTS OF WEST KENT

35 pressed plants collected recently were exhibited. Those from Swanscombe included *Vicia lutea, V. tenuifolia, Lathyrus hirsutus, Trifolium aureum* and *Pyrola rotundifolia subsp. maritima* (the latter thought to be new to eastern Britain). *Vicia lutea* was also shown from Swanley and Woolwich Common; together with *Trifolium hybridum* subsp. *elegans* from Wrotham Hill.

A number of naturalized rosaceous shrubs were exhibited: *Cotoneaster acutifolius, C. divaricatus, C. conspicuus, C. adpressus* var. *praecox, C. horizontalis* var. *robustus, Crataegus crus-galli, C. prunifolia, C. ovalifolia, C. pedicillata* and *Sorbaria arborea*. Other naturalized shrubs were *Buddleia alternifolia, Laburnum alpinum, Forsythia suspensa, Choisya ternata* and the One-leaved Ash.

Other garden plants naturalized included *Peltiphyllum peltatum*, *Campanula glomerata* subsp. *elliptica*, and the two grasses *Bromus carinatus* and *B. pumpellianus*. *Cyclamen graecum* was from a patch naturalized on Dartford Heath, and *Amaranthus bouchonii* was from Plumstead Marshes.

A plant from Scilly was also exhibited – *Euphorbia mellifera* naturalized on walls on Tresco in 1971.

J. R. PALMER

THE SPREAD OF *EPILOBIUM CILIATUM* RAFIN. IN THE BRITISH ISLES

The willow-herb *Epilobium ciliatum* Rafin. (*E. adenocaulon* Hausskn.) is native to North America, but it is now widely naturalized in Europe. It was first collected in Britain in the late 19th century, but was not recognized until the 1930s. Since then it has spread rapidly, and in many areas of southern England it is the commonest species of *Epilobium*. The spread of the species was illustrated by a series of distribution maps. These showed the initial colonization of south-eastern England, followed by an advance northwards and westwards. There is little evidence of the discontinuous pattern of spread which has been noted for some other alien species.

C. D. Preston

SOME COASTAL ECOTYPIC VARIANTS IN THE BRITISH ISLES

Many widespread or common plant species are represented in different habitats by distinct variants. Several species that are present on the coast (where selection pressures can be severe) and also at inland sites have ecotypic variants in each type of habitat. Experimental studies have often revealed genetic differences between such variants that may be maintained over many years or generations in cultivation. A recent survey by one of us (J. R. A. in press) showed that there are just over 120 coastal ecotypic variants documented from Europe and the Mediterranean region, the great majority being described from north-western parts of Europe.

Three examples of dwarfed, coastal ecotypic variants from the British Isles were exhibited: *Serratula tinctoria* var. *reducta* Rouy, *Stachys officinalis* [*Betonica officinalis* L.] var. *nana* Druce and *Vicia sylvatica* var. *condensata* Druce. Comparative coastal and inland herbarium material was displayed, together with distribution maps.

C. D. Preston & J. R. Akeroyd

GYNODIOECY IN *SAXIFRAGA GRANULATA*

The occurrence of male-sterile (female) variants of *Saxifraga granulata* L. was first reported by Marsden-Jones & Turrill (*J. Genet.* **48**: 206–218, 1947) from a population near the Hog's Back, near Guildford, Surrey (v.c. 17). We have found two further populations at Staindrop, Co. Durham (v.c. 66) and near Macclesfield, Cheshire (v.c. 58) which contain significant numbers of female plants together with normal hermaphrodites. A few intermediate plants, which bear some normal and some aborted anthers, were also found.

Populations polymorphic for male-sterile and male-fertile plants are referred to as gynodioecious, and pose an interesting evolutionary problem. Females are expected to be at a selective disadvantage compared with hermaphrodites, because they contribute no genes to the next generation via pollen. Therefore, we should expect them to show some balancing advantage over hermaphrodites. They could set more seed than hermaphrodites, be more vigorous vegetatively, or produce offspring sexually which are of superior fitness to those of hermaphrodites, because of inbreeding depression in the latter.

Our data on the reproductive performances of hermaphrodites and females from Staindrop suggest that females actually set less seed than hermaphrodites, probably because they receive insufficient pollen. Inbreeding depression in the seed progeny of hermaphrodites is the force maintaining the gynodioecious polymorphism in *S. granulata*.

A. J. Richards & D. P. Stevens

CORNFLOWERS

Cornfield weeds include some of Britain's most attractive and coveted wildflowers, but also comprise our most threatened plant communities. Many factors have contributed to their decline, including improved seed purity, disruption of rotation and loss of fallow, cultivation of winter cereals, increased use of fertilizers and herbicides, widespread stubble burning, modification of soils, and destruction of field margins. These factors are poorly understood, but they are evidently causing profound changes to habitats and will result in the loss of all but the most ecologically-tolerant arable species. Most have declined so rapidly that current knowledge of their distributions is outdated and the plight of many is seriously underestimated: a nationwide survey of arable floras is urgently required.

J. ROBERTSON & R. M. BATEMAN

THE AVON FLORA PROJECT

The task of producing a mapped vascular Flora for the county of Avon was begun in autumn 1983. Since White's *The Bristol Flora* (1912) there has been no Flora written using boundaries approximating to those of Avon today. Avon has never been mapped floristically.

After one year of a 5–6 year project a system for recording, a network of recorders, and a computerized data storage and access system have been established. The project is to use the one-kilometre square as a basis for recording, and is to be based on the Bristol Regional Environmental Records Centre; and for the second year it has a Manpower Services Commission team to both co-ordinate and record for it. These three aspects of the project are unusual and produce special conditions for the production of a County Flora.

P. G. ROONEY

WHAT IS YOUR LOCAL *LONICERA*?

Dunbartonshire (v.c. 99) *Lonicera* species seem rarely to be *L. periclymenum* L. Non-*periclymenum* types occur southwards to Wigtonshire (v.c. 74). Horticultural and botanical literature shows great confusion, 'wild' plants clearly being of garden origin or hybrids. One v.c. 99 plant may be *L. periclymenum* × *L. caprifolium* L.

The anthocyanin-content of these un-named Loniceras varies; some are pale-flowered and glaucous, but most have dark leaves, ruby-tinted flowers, purple-red, strong sterile shoots with 'bloom'. They have certain features distinguishing them from *L. periclymenum*: they seldom climb, are exceedingly robust and sun-loving. The foliage is leathery, usually hairless, broad, with occasionally small axilliary leaves below the flower-heads, often sub-perfoliate. Flowers are glandular-haired, carnation- or rose-scented, the buds tinted red, green or rose, and more numerous. True wild honesuckle seems very scarce in western Scotland. It is hoped the extent of the unknown Loniceras will be discovered when other populations are inspected.

A. RUTHERFORD

A SCANNING ELECTRON MICROSCOPE STUDY OF BRITISH *FUMARIA* SPECIES

The ten British species of *Fumaria* show individually distinct fruit shapes and degrees of fruit-coat ornamentation. The fruits of the British species were examined with the aid of the SEM: a full account of this study is available in the author's Ph.D. thesis (Bristol University, 1984). The SEM has proved to be a powerful tool in the elucidation of details of the *Fumaria* periderm that had not previously been described, and provides an accurate portrayal of the fruit shapes.

P. L. SMITH

A SCOTTISH MISCELLANY

The following were exhibited:
(a) New records from Scotland, including a specimen of *Carex divulsa* subsp. *leersii* from near Aberlady (v.c. 82), the third Scottish record; the previous ones were from near Lauder (v.c. 81) and near Newbattle (v.c. 83). *Oenothera* × *fallax* is new to v.c. 73 and *Cerastium* × *maureri* at Borthwick (v.c. 83) is new to Scotland.
(b) *Cardamine amara*, with deep pink petals, found in a marsh near Borthwick (v.c. 83), was shown and also a specimen of *C. amara* var. *lilacina* from v.c. 88 and one of var. *erubescens* to show the colour variation that is occasionally found in this species.

O. M. Stewart

PAINTINGS OF WILD FLOWERS

Painting of orchids and legumes from a holiday in Tuscany were exhibited, together with paintings of hawkweeds from the 1984 B.S.B.I. field meeting at Braemar (v.c. 92) and aliens from the tannery at Grampound (v.c. 1).

O. M. Stewart

THE THOMPSON TOUCH

The exhibit consisted of 13 drawings of plants from West Kent, the Lizard in Cornwall, and East Suffolk. The drawings were as follows. West Kent: *Cotoneaster divaricatus, C. adpressus* var. *praecox, C. dammeri* 'Coral Beauty', *Myrtus ugni, Ligustrum lucidum, Trifolium aureum, Bidens connata*. East Suffolk: *Agrostemma githago, Cynoglossum officinale, Geranium dissectum, Lathyrus nissolia, Bryonia dioica*. The Lizard: *Trifolium occidentale*.

H. Thompson

RANUNCULUS PENICILLATUS (DUMORT.) BAB. IN BRITAIN AND IRELAND

Herbarium specimens, photographs and distribution maps of the varieties of *R. penicillatus* were exhibited. Var. *penicillatus* differs from var. *calcareus* (Butcher) Cook and var. *vertumnus* Cook in producing entire leaves, whilst the latter two varieties intergrade morphologically. Vars *calcareus* and *vertumnus* have been found sharing a habitat in base-rich rivers, whereas var. *penicillatus* appears to be calcifuge. This variety occupies a number of base-poor rivers both in western Britain and in Ireland, whereas vars *calcareus* and *vertumnus* are not known from Ireland. Thus, in addition to the morphological discontinuity between var. *penicillatus* on the one hand, and vars *calcareus* and *vertumnus* on the other, var. *penicillatus* is distinct ecologically and may have a different, if overlapping, distribution from the other two varieties. Further field data are needed.

S. D. Webster

MEXICAN TEA BREWING IN EAST LONDON

In September 1984, a vigorous colony of *Chenopodium ambrosioides* var. *ambrosioides* was found extending along the River Lea Canal towpaths from Hackney Wick to Bromley-by-Bow. Several thousand plants were observed, some very large. To date, *C. ambrosioides* (more usually as var. *anthelminticum*) has been recorded several times as a casual of refuse or shoddy, but never before as a firmly established alien. Its success must owe much to London's recent hot summers, frost-free autumns, and water-borne seed distribution. Known as Mexican Tea, this pungently aromatic tropical species is of high medicinal repute in the Americas, where it is cultivated as a vermifuge. Fresh specimens were displayed.

B. WURZELL

CONYZA SUMATRENSIS NATURALIZED IN SOUTHERN ENGLAND

Conyza sumatrensis, as distinct from *C. bonariensis*, is now recognized as new to the British mainland. Previously it was known to be widespread in France and the Channel Islands. From September to November 1984, approximately 20 colonies were found established throughout East London, suggesting a recent westward invasion along the Thames from S.E. Essex where it had been earlier reported as *C. bonariensis*. It is now a conspicuous and ecologically important part of the London flora, especially where wastelands offer old concrete, stone, or brick crevices to meet its high heat requirement. Herbarium specimens of *C. sumatrensis* and related taxa, from London, Jersey, Paris, and California, were shown, and a key was given to distinguish all species and varieties now found in Britain.

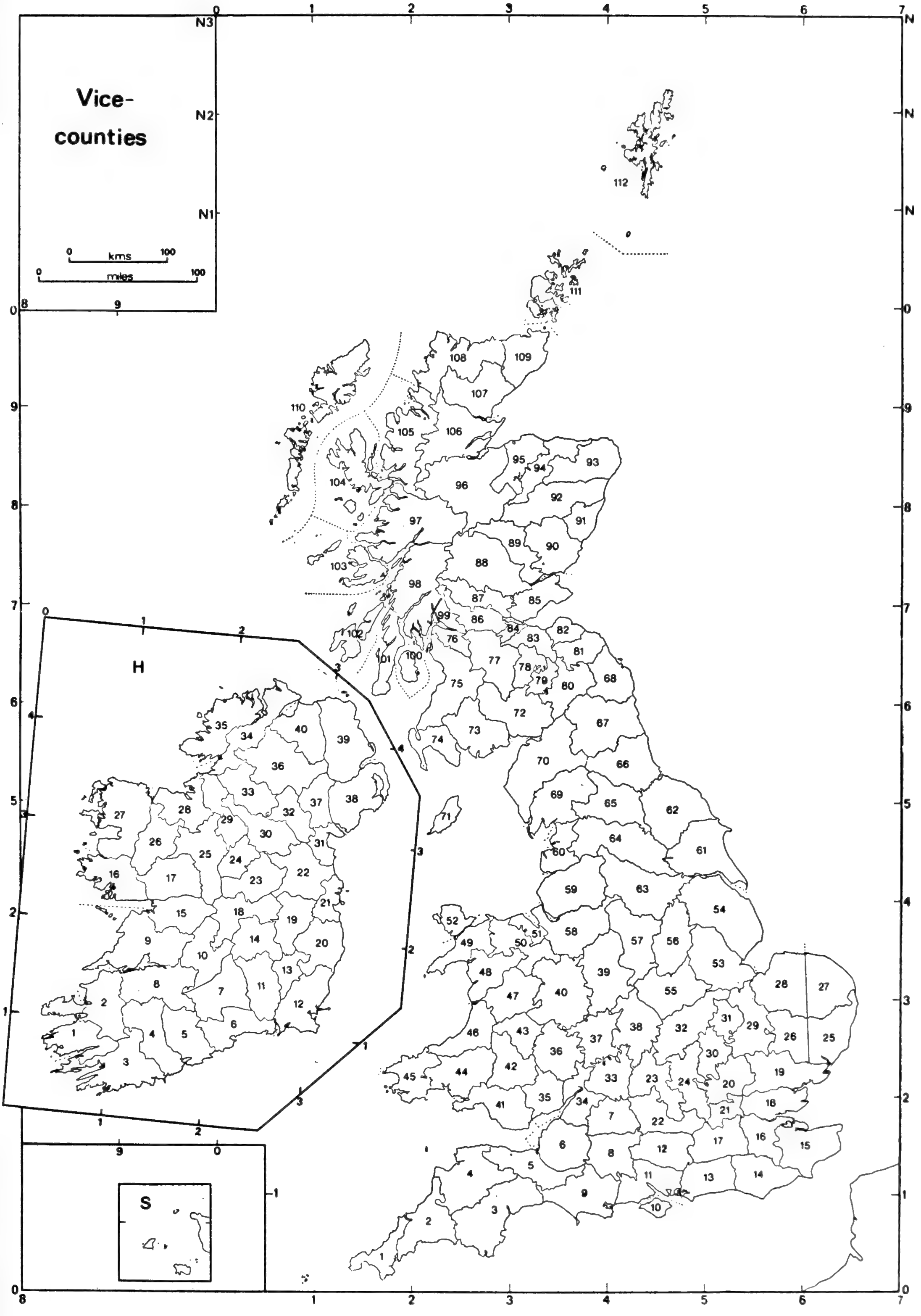
B. WURZELL

The following also exhibited:
- S. BELL & G. WHITE. Macrophyte survey of freshwater lochs, Inverpolly National Nature Reserve, Wester Ross.
- BOTANY LIBRARY, BRITISH MUSEUM (NATURAL HISTORY). Recent botanical books, and conservation of Botany Library collections.
- R. FITZGERALD & J. BEVAN. *Sorbus porrigentiformis* E. F. Warb. in v.c. 5.
- A. N. GIBBY. Botanical postage stamps, including some showing medicinal plants.
- *HIERACIUM* STUDY GROUP. *Hieracium lasiophyllum* Koch in v.c. 4.
- M. INGROUILLE. The *Salicornia* problem.
- Q. O. N. KAY. Trioecy in *Cirsium arvense* (L.) Scop.
- F. LE SUEUR. A new Flora of Jersey.
- C. SAUNDERS & ST CHRISTOPHER'S SCHOOL, BURNHAM-ON-SEA. Operation Orchid.
- P. TAYLOR. A photographic botanical excursion.
- J. TUBBS. A year's flora through my lens.

In the lecture hall, the following members gave short talks illustrated by colour slides:
- S. BELL & G. WHITE. Underwater photography – a diver's-eye view of freshwater macrophytes in Scottish lochs.
- C. A. CHADWELL. Arctic-alpines and cosmopolitan weeds of Britain and the North-West Himalaya.
- R. W. DAVID. Uncommon British sedges.
- V. FLEMING. Crete.
- F. LE SUEUR. Slides to celebrate the new *Flora of Jersey*.
- A. J. RICHARDS. Some uncommon plants of the Northumberland whinstone.
- F. ROSE. B.S.B.I. excursion to Normandy, July 1984.
- F. H. PERRING. Some examples of British species in north-eastern China.

BOTANICAL SOCIETY OF THE BRITISH ISLES, COMMITTEE FOR SCOTLAND, AND BOTANICAL SOCIETY OF EDINBURGH, EXHIBITION MEETING, 1984

An Exhibition Meeting was held in conjunction with the Glasgow Natural History Society on Saturday, 3rd November 1984, in the Department of Botany, University of Glasgow. Events included: a series of exhibits and a slide show; a meeting of Scottish vice-county recorders, addressed by Mrs Mary Briggs; the Annual General Meeting of B.S.B.I. members resident in Scotland; and a lecture by Miss Lynne Farrell entitled "Rare plant surveying".


Vice-
counties
0 kms 100
0 miles 100
N3
N2
N1
N
H
S
0
1
2
3
4
5
6
7
8
9
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91
92
93
94
95
96
97
98
99
100
101
102
103
104
105
106
107
108
109
110
111
112

NAMES OF VICE-COUNTIES IN *WATSONIA*

ENGLAND, WALES AND SCOTLAND

1. W. Cornwall
1b. Scilly
2. E. Cornwall
3. S. Devon
4. N. Devon
5. S. Somerset
6. N. Somerset
7. N. Wilts.
8. S. Wilts.
9. Dorset
10. Wight
11. S. Hants.
12. N. Hants.
13. W. Sussex
14. E. Sussex
15. E. Kent
16. W. Kent
17. Surrey
18. S. Essex
19. N. Essex
20. Herts.
21. Middlesex
22. Berks.
23. Oxon
24. Bucks.
25. E. Suffolk
26. W. Suffolk
27. E. Norfolk
28. W. Norfolk
29. Cambs.
30. Beds.
31. Hunts.
32. Northants.
33. E. Gloucs.
34. W. Gloucs.
35. Mons.
36. Herefs.
37. Worcs.
38. Warks.
39. Staffs.
40. Salop
41. Glam.
42. Brecs.
43. Rads.
44. Carms.
45. Pembs.
46. Cards.
47. Monts.
48. Merioneth
49. Caerns.
50. Denbs.
51. Flints.
52. Anglesey
53. S. Lincs.
54. N. Lincs.
55. Leics.
55b. Rutland
56. Notts.
57. Derbys.
58. Cheshire
59. S. Lancs.
60. W. Lancs.
61. S.E. Yorks.
62. N.E. Yorks.
63. S.W. Yorks.
64. Mid-W. Yorks.
65. N.W. Yorks.
66. Co. Durham
67. S. Northumb.
68. Cheviot
69. Westmorland
69b. Furness
70. Cumberland
71. Man
72. Dumfriess.
73. Kirkcudbrights.
74. Wigtowns.
75. Ayrs.
76. Renfrews.
77. Lanarks.
78. Peebless.
79. Selkirks.
80. Roxburghs.
81. Berwicks.
82. E. Lothian
83. Midlothian
84. W. Lothian
85. Fife
86. Stirlings.
87. W. Perth
88. Mid Perth
89. E. Perth
90. Angus
91. Kincardines.
92. S. Aberdeen
93. N. Aberdeen
94. Banffs.
95. Moray
96. Easterness
96b. Nairns.
97. Westerness
98. Main Argyll
99. Dunbarton
100. Clyde Is.
101. Kintyre
102. S. Ebudes
103. Mid Ebudes
104. N. Ebudes
105. W. Ross
106. E. Ross
107. E. Sutherland
108. W. Sutherland
109. Caithness
110. Outer Hebrides
111. Orkney
112. Shetland

IRELAND

H1. S. Kerry
H2. N. Kerry
H3. W. Cork
H4. Mid Cork
H5. E. Cork
H6. Co. Waterford
H7. S. Tipperary
H8. Co. Limerick
H9. Co. Clare
H10. N. Tipperary
H11. Co. Kilkenny
H12. Co. Wexford
H13. Co. Carlow
H14. Laois
H15. S.E. Galway
H16. W. Galway
H17. N.E. Galway
H18. Offaly
H19. Co. Kildare
H20. Co. Wicklow
H21. Co. Dublin
H22. Meath
H23. Westmeath
H24. Co. Longford
H25. Co. Roscommon
H26. E. Mayo
H27. W. Mayo
H28. Co. Sligo
H29. Co. Leitrim
H30. Co. Cavan
H31. Co. Louth
H32. Co. Monaghan
H33. Fermanagh
H34. E. Donegal
H35. W. Donegal
H36. Tyrone
H37. Co. Armagh
H38. Co. Down
H39. Co. Antrim
H40. Co. Londonderry

INSTRUCTIONS TO CONTRIBUTORS

Papers and Short Notes concerning the systematics and distribution of British and European vascular plants as well as topics of a more general character are invited.

Manuscripts must be submitted in duplicate, typewritten on one side of the paper only, with wide margins and double-spaced throughout. They should follow recent issues of *Watsonia* in all matters of format, including abstracts, headings, tables, keys, figures, references and appendices. Note particularly use of capitals and italics. *Only underline where italics are required.*

Tables, appendices and captions to figures should be typed on separate sheets and attached at the end of the manuscript. Names of periodicals in the references should be abbreviated as in the *World list of scientific periodicals*, and herbaria as in Kent & Allen's *British and Irish herbaria*. Line drawings should be in Indian ink, preferably on good quality white card, but blue-lined graph paper or tracing paper is acceptable. They should be drawn at least twice the final size and they will normally occupy the full width of the page. Lettering should be done in Lettraset or by high-quality stencilling, though graph axes and other more extensive labelling are best done in pencil and left to the printer. Photographs can be accepted only in exceptional cases.

Contributors are strongly advised to consult the editors before submission in any cases of doubt. Manuscripts will be scrutinized by the editors and a referee and a decision communicated as soon as possible. Authors receive a galley proof for checking, but only errors of typography or fact may be corrected. 25 offprints are given free to authors of papers and Short Notes. Further copies may be purchased in multiples of 25 at the current price.

The Society takes no responsibility for the views expressed by authors of articles.

Papers and Short Notes should be sent to Dr R. J. Gornall, Botany Department, The University, Leicester, LE1 7RH. Books for review should be sent to Dr N. K. B. Robson, Botany Department, British Museum (Natural History), Cromwell Road, London, SW7 5BD. Plant records should be sent to the appropriate vice-county recorders. Reports of field meetings should be sent to Dr B. S. Rushton, Biology Department, The University of Ulster, Coleraine, Co. Londonderry, Ireland.

Watsonia

July 1985 Volume fifteen Part four

Contents

Published by the Botanical Society of the British Isles

UK ISSN 0043-1532

Filmset by
WILMASET, BIRKENHEAD, MERSEYSIDE
Printed in Great Britain by
EATON PRESS LIMITED, WESTFIELD ROAD, WALLASEY, MERSEYSIDE

WATSONIA

JOURNAL AND PROCEEDINGS OF THE BOTANICAL SOCIETY OF THE BRITISH ISLES

VOLUME 15

EDITED BY

J. R. AKEROYD, S. M. EDEN, R. J. GORNALL,

C. D. PRESTON AND N. K. B. ROBSON

1984–85

PRINTED FOR THE SOCIETY BY
Eaton Press Limited, Wallasey, Merseyside

PUBLISHED AND SOLD BY THE BOTANICAL SOCIETY OF THE BRITISH ISLES,
C/O DEPARTMENT OF BOTANY, BRITISH MUSEUM (NATURAL HISTORY), LONDON SW7 5BD

CONTENTS

PAGES

Short notes:

Reports

Short notes:

Reports

Short notes

Reports

Short notes

Reports